

**Post-Release Performance of Natural and Hatchery Subyearling Fall Chinook
Salmon in the Snake and Clearwater Rivers**

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EXECUTIVE SUMMARY

In 2005, we initiated a multi-year study to compare smolt-to-adult return rates (SARs) of Snake River Basin fall Chinook salmon *Oncorhynchus tshawytscha* that were transported or allowed to migrate inriver through the hydropower system. Fish were designated for transportation or inriver migration prior to release and arrival at Lower Granite Dam. As fish from either study group entered the bypass system at each collector dam, they were either transported or returned to the river, depending on the previous designation. This study design produced comparable groups to evaluate the effect of dam operations under both a maximized transport and a maximized inriver migration strategy.

Because there were not enough natural subyearlings available for tagging to calculate precise SARs, we tagged "surrogate" subyearlings of Lyons Ferry Hatchery origin. Surrogate subyearling growth is slowed at the hatchery so that released fish match natural subyearlings in size. Surrogates are released directly into the river during the peak rearing period of natural subyearlings, from late May to early July. The study was conducted in 2005, primarily with surrogate subyearlings, but some natural and production subyearlings were also tagged with passive integrated transponder (PIT) tags as part of other long-term research. Production subyearlings are grown rapidly and usually acclimated prior to release, which occurs from April to June depending on location and year.

Evaluation of the two migration strategies will depend on adult returns in future years. Here we report results where we compared post-release attributes among fish from an additional study to the inriver migrant component of the transportation study. This group included PIT-tagged natural, surrogate, and production subyearling Chinook salmon. Attributes were evaluated as fish passed downstream through the hydropower system in 2005 to compare the performance of surrogate and production fall subyearling Chinook with that of natural fall subyearling Chinook.

Post-release attributes compared were 1) passage timing at select dams, 2) level of exposure to summer spill, 3) travel time, 4) size during seaward migration, and 5) joint probability of active migration and survival. We found these attributes were more similar between natural and surrogate subyearlings than between natural and production subyearlings, and we discuss options for increasing this similarity.

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INTRODUCTION

In 2005, the U.S. Army Corps of Engineers initiated a cooperative study among the National Marine Fisheries Service, Nez Perce Tribe Department of Fisheries Resources Management, and U.S. Fish and Wildlife Service Idaho Fishery Resource Office. These agencies were contracted to compare the smolt-to-adult return rates (SARs) of Snake River Basin fall Chinook salmon *Oncorhynchus tshawytscha* that were either transported or migrated in the river. Study fish were designated for inriver migration or transportation prior to release, and when collected in the bypass system at dams were either transported or returned to the river, depending on their prior designation (Marsh and Connor 2004).

This study was coordinated with an inter-agency and tribal team, including representatives of the Bonneville Power Administration, Columbia River Intertribal Fish Commission, Idaho Department of Fish and Game, Oregon Department of Fish and Wildlife, Umatilla Tribe, and Washington Department of Fish and Wildlife. Study results are intended to be applicable to management of the natural Snake River Basin fall Chinook salmon population, with primary emphasis on subpopulations in the Snake and Clearwater Rivers.

Because salmonids generally experience low SARs, large numbers of fish are required to calculate precise ratios of SARs between treatment groups. Naturally spawning fall subyearling Chinook salmon are not normally available in these numbers. Therefore, to compare SARs of different treatment groups for this study, our only option for tagging sufficient numbers of fish was to use production or surrogate subyearlings in addition to natural fish (Figure 1).

Hatchery production subyearlings are grown rapidly and usually acclimated prior to release from April to June depending on location and year. Surrogate subyearling growth is slowed at the hatchery to match size at release to that of natural subyearlings. Surrogates are released throughout the peak rearing period of natural subyearling Chinook parr, from late May to early July. Fish tagged with passive integrated transponder (PIT) tags (Prentice et al. 1990a) for this study were primarily surrogate subyearling Chinook, but some natural and production subyearling Chinook salmon were also tagged as part of other long-term research.

Evaluation of the two migration strategies will depend on adult returns in future years and will not be reported here. This report describes lower Snake River passage of the inriver migrant component of natural and surrogate fall Chinook salmon tagged for the transportation study. We also compare post-release attributes of natural, surrogate, and production subyearlings released in 2005 as they passed downstream through the hydropower system. We evaluate the performance of surrogate and production

subyearlings compared to that of natural subyearling fish. Finally, we use these results to identify methods to increase the similarity between natural and surrogate subyearling fall Chinook.

To accomplish these study objectives, we compared the following post-release attributes among the three groups released into the Snake and Clearwater Rivers in 2005:

- 1) Passage timing at Lower Granite, Little Goose, and Lower Monumental Dams
- 2) Level of exposure to summer spill at these three dams
- 3) Travel time to Lower Monumental Dam
- 4) Size during seaward migration
- 5) Joint probability of active migration and survival to the tailrace of Lower Monumental Dam.

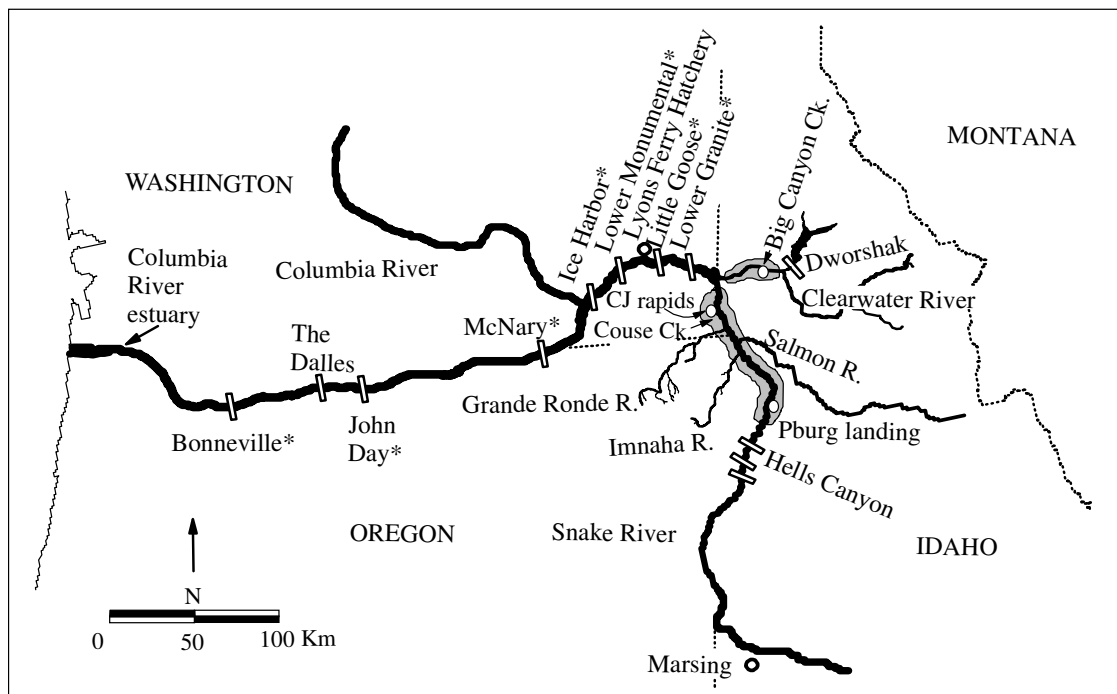


Figure 1. The reaches of the Snake and Clearwater Rivers where natural fall Chinook salmon subyearlings were captured, PIT tagged, and released (shaded). The release locations of PIT-tagged surrogate subyearlings at Couse and Big Canyon creeks. Snake River production subyearlings were released at Hells Canyon Dam, Pittsburg Landing and Captain John Rapids acclimation facilities, and Couse Creek. The Clearwater River production subyearlings were released from Big Canyon Creek acclimation facility. Dams with juvenile fish bypass systems and PIT-tag detection systems are indicated by an asterisk.

METHODS

Fish Collection, Tagging, and Release

Natural Subyearling Fall Chinook

Snake River--Idaho Fishery Resource Office personnel used a beach seine to capture subyearling fall Chinook at sites in the free-flowing Snake River, as described by Connor et al. (1998, 2002). Sampling began at the onset of fry emergence in late March and was conducted 3 d/week. A total of 15 permanent stations from rkm 227 to 366 (rkm 0 = Snake River mouth) were sampled every week. During 15 May-6 June, supplemental stations were sampled to increase the number of natural subyearlings PIT tagged. Sampling was discontinued after the first week in July, when catch was near zero.

Origin (hatchery vs. natural) of unmarked (i.e., adipose fin not clipped) and non-tagged fish (i.e., no coded wire or PIT tag) was determined based primarily on pupil diameter and body shape. Natural fish had smaller pupils and were more robust than their hatchery counterparts. Each natural subyearling fall Chinook salmon captured was anesthetized in a 3-mL MS-222 stock solution (100 g/L) per 19 L of water buffered with a sodium bicarbonate solution, measured to fork length (FL, in mm), and a tissue sample was collected for future genetic analyses. Natural subyearlings 60-mm and longer were implanted with a PIT tag and released at the collection site after a 15-min recovery period.

Clearwater River--The Nez Perce Tribe used beach seines, fyke nets, and rotary screw traps to capture fall Chinook subyearlings in the lower Clearwater River. Seining was conducted during 3 May–1 August along the lower Clearwater River from rkm 7 to 65. Permanent sites were seined 5 d/week when flow allowed. Supplemental sites were seined when time and flow allowed. Two sizes of beach seines fitted with 0.48-cm diameter mesh were used (30.5 × 1.8 m and 15.2 × 1.2 m). Both were fitted with weighted multistranded mud lines. The larger seine was set from a jet boat, and the smaller seine set by hand at less accessible and smaller sites. A total of four fyke nets were tested 23 June and 6 July. Two 2.4-m diameter rotary screw smolt traps arrived late in the season and were suspended from a railroad bridge along both the north and south shorelines at rkm 20 from 30 June to 4 August. Beach seining and screw trapping were discontinued the first week in August, when catch was near zero.

Origin was determined as described for the Snake River. All salmonids captured by all methods were placed in 18.9-L buckets and then in larger, aerated 114-L plastic holding bins. Salmonids were anesthetized in a 3-mL MS-222 stock solution (100 g/L) per 19 L of water buffered with a sodium bicarbonate solution. All natural fall Chinook were measured to the nearest 1.0 mm FL and weighed to the nearest 0.1 g. Tissue samples were collected (non-lethal upper caudal fin clip) from a random subsample of natural fish for future genetic analyses. Natural fall Chinook salmon 60-mm FL and longer were implanted with PIT tags and released at the collection site after a 15-min recovery period.

Surrogate Subyearling Fall Chinook

Snake River--Approximately 400,000 subyearlings were cultured at Lyons Ferry Hatchery by the Washington Department of Fish and Wildlife. Fish were raised to 85-90 mm for direct release at Captain John Rapids in late May (Connor et al. 2004). Acquisition of approximately 176,000 of these subyearlings for 2005 surrogate releases was coordinated in accordance with the draft fall Chinook salmon production plan of the Production Advisory Committee of *U.S. v. Oregon* (Table B4, Production Priority 8).

In March, the Dworshak Fish Health Laboratory examined 60 randomly selected subyearlings being reared for the surrogate releases at Lyons Ferry Hatchery for *Renibacterium salmoninarum* antigen by ELISA. In addition, gill/kidney/spleen tissue was examined for viruses associated with infectious pancreatic necrosis, infectious hematopoietic necrosis, and viral hemorrhagic septicemia. The ELISA results were low (optical density less than 0.09), and viral tests were negative.

After disease testing was completed, Idaho Fishery Resource Office personnel transported approximately 176,000 surrogates from Lyons Ferry to Dworshak National Fish Hatchery using a truck equipped with a 7,500-L tank. Oxygen in the tank was kept near 100% saturation during each 3-h trip, with one trip each day during 11-13 April 2005. Average fish length was 60 mm FL, and loading density¹ was 0.02 kg/L, well below the recommended maximum of 0.24 kg/L for Chinook salmon (Piper et al. 1982).

Upon arrival at Dworshak, surrogates were piped from the tank into three separate 48-m³ raceways supplied with 5.6°C water at approximately 1,136 L/min. Starting fish

¹ Loading density = kg of fish/(tank capacity in L - water displaced by fish in kg).

densities ranged from 3.9 to 4.3 kg/m³. Each raceway was treated with 45 kg of coarse water softening salt (NaCl) immediately after fish were transferred, after weekly cleaning, and after crowding during tagging. Surrogates were initially fed No. 2 crumb BioDiet starter.² Feed size was increased to No. 1.5 BioDiet growth formula as surrogates grew. Feeding rates varied from 2 to 4% to achieve a mean size at release of 70-75 mm FL. On 26 April, surrogates in each raceway were treated for a minor outbreak of tail fungus. Treatment involved turning off flow and then adding 45 kg of coarse water softener salt and 7.6 L of formalin to each raceway. Oxygen was monitored throughout the 1-h treatment and never fell below 70% saturation. There were no bacterial or viral epizootics during rearing.

Surrogates were taken off feed 24 to 48 h before tagging. Final rearing density in the raceways before tagging ranged from 4.9 to 6.3 kg/m³, well below densities reported to adversely affect adult returns of Chinook salmon (see Martin and Wertheimer 1989; Banks 1994; Ewing and Ewing 1995). Temperatures in the raceways during tagging ranged from 6.8 to 7.9°C. Tagging of surrogates began on 16 May and was scheduled to occur daily during three periods: 16-20 May, 23-27 May, and 30 May-3 June. These periods coincided with the historical peak rearing period of natural parr in the Snake River (Connor et al. 2002).

Each morning, surrogates in the raceway designated for tagging were crowded and then bucketed to a 1,893-L holding tank, which was supplied with raceway water and located inside a self-contained tagging trailer. Immediately before tagging, surrogates were transferred to a 379-L sink containing anesthetic water (45–50 mg/L MS-222). The water was recirculated through a 10-25 µm filter to remove particulate matter and then exposed to an ultraviolet light filter to prevent viral and bacterial infections. Surrogates smaller than 60-mm FL or with obvious signs of disease or injury were rejected for tagging and piped back to an unoccupied raceway.

Biomark, Inc. was contracted to implant the surrogates with 134.2-kHz ISO PIT tags (TX1400ST) using a modified syringe tipped with a 12-gauge hypodermic needle (Prentice et al. 1990a). Used needles were disinfected in a 70% alcohol solution for approximately 10 min before reuse. After tagging, each fish was measured (FL, mm) and each day a subsample of approximately 100 fish was wet weighed to the nearest 0.1 g. Fish were then piped to a transport truck equipped with a 1,800-L tank constantly supplied with fresh raceway water until tagging was completed.

² Use of trade names does not imply endorsement by the U.S. National Marine Fisheries Service, U.S. Fish and Wildlife Service, or Nez Perce Tribe.

After tagging was completed each day, National Marine Fisheries Service staff trucked surrogates to the mouth of Couse Creek, located 254 km upstream from the Snake River mouth. During each 2-h trip to Couse Creek, oxygen in the tank was kept near 100% saturation. Loading density ranged from 0.02 to 0.05 kg/L. Surrogates were acclimated to ambient river temperature (range, 11.5–13.6°C) using a gasoline-powered water pump to gradually replace the raceway water in the tank with river water at a maximum rate of 2°C warming per hour.

Subyearlings were released directly to the Snake River via a flexible hose when tank temperature equaled river temperature, which generally occurred from late afternoon to near dusk. Staff observed surrogates for mortality throughout tagging and release, and pre-release mortality ranged from 0.02 to 0.3%. The tank was inspected for shed tags after fish were released, and shedding ranged from 0.1 to 0.6%.

Clearwater River--A critical component of the 2005 study was to represent the population of fall Chinook salmon subyearlings by releasing surrogates into both the Snake and Clearwater Rivers in proportion to previous redd counts in each drainage. Based on these counts, we assumed the Snake River drainage accounted for 70% and the Clearwater River drainage 30% of all redds (70:30 rule). However, preliminary information indicated that the average size of surrogates to be provided for release would be greater than 60-mm FL by April. Thus, it seemed unlikely that we could limit growth sufficiently to provide 70-75 mm surrogates for release into the Clearwater River during the 3-week period of 20 June to 8 July, the period of peak rearing for natural subyearling parr (Connor et al. 2002; Nez Perce Tribe, unpublished data).

We provided for a small-scale experimental release of Clearwater River surrogates by transferring approximately 4,000 excess fry from Lyons Ferry Hatchery to Dworshak National Fish Hatchery on 24 February. After transfer, fry were reared in a 1.6-m³ circular tank supplied with 6.8–11.6°C water at 39 L/min and fed at 1.7% body weight. Feed size was later increased with fish size, as described for Snake River surrogates. Density in the circular tank from 24 February to 17 June ranged from 1.5 to 9.2 kg/m³.

Because subyearlings were from multiple egg takes at Lyons Ferry Hatchery, fork length at the time of transfer from Lyons Ferry Hatchery in April varied markedly. Thus we were able to make a full release of Clearwater River surrogates in 2005. All Snake River surrogates that were large enough to PIT tag had been tagged by 27 May (i.e., one week earlier than planned), leaving approximately 45,000 fish available for releases. These Clearwater River surrogates had been routed to a single raceway during tagging of

the Snake River surrogates and were reared to a maximum density of 4.5 kg/m³ at temperatures of 7.9-9.0°C. The 4,000 fish reared in the circular tank were transferred to a second raceway on 17 June and reared to a maximum density of 0.4 kg/m³, bringing the total number of fish available for release into the Clearwater River to approximately 49,000.

Clearwater River surrogates were fed, handled, tagged, and released as described for Snake River surrogates with the following six exceptions. Clearwater River surrogates were:

- 1) graded by use of a hand-held device into a second raceway 48 h before tagging to minimize the number of fish less than 60-mm FL that were bucketed to the trailer;
- 2) tagged and released 4 d/week for 3 weekly periods: 21-24 June, 27 June-2 July, and 5-8 July;
- 3) released at Big Canyon Creek 57 km upstream from the Clearwater River mouth;
- 4) transported at loading densities of 0.1 kg/L;
- 5) transported for only 20-30 min to reach the release site; and
- 6) acclimated and released at temperatures ranging from 15.0 to 17.2°C.

Production Subyearling Fall Chinook

We contacted researchers coordinating the PIT tagging of production subyearlings in 2005 and received permission to use their PIT-tag data in our analyses. Snake River production subyearlings were all of Lyons Ferry Hatchery origin. They were PIT tagged with standard methods by the agencies referenced below. Idaho Fish and Game received fertilized gametes that were reared to production size at Oxbow Hatchery prior to being directly released at Hells Canyon Dam.

Oregon Department of Fish and Wildlife at Umatilla Hatchery also received fertilized gametes that were reared to production size prior to being transferred by the Nez Perce Tribe to the Pittsburg Landing acclimation facility. Washington Department of Fish and Wildlife trucked production subyearlings from Lyons Ferry Hatchery to Couse Creek for direct release. The Nez Perce Tribe received production subyearlings for acclimation and release at Captain John Rapids acclimation facility and Big Canyon Creek acclimation facility. See McCleod (2006) for additional information on these acclimation facilities.

Detection of PIT-Tagged Fish

At Lower Granite Dam, PIT-tagged fish that were collected by fish guidance screens were routed to the juvenile bypass system (Prentice et al. 1990b). Study fish designated for transport were routed to barge holding raceways, while those designated for inriver migration were routed back to the river. Fish were routed using automated slide gates that directed a fish based on its PIT-tag code (Marsh et al. 1999; Downing et al. 2001). Thus, a predetermined random sample (natural and surrogate) or the majority by default (production) of the PIT-tagged subyearlings were returned to the river.

The PIT-tagged subyearlings continued migration in the river if they were routed from the bypass system back to the river, if they passed Lower Granite Dam under submersible traveling screens and through turbines, or if they passed via the spillways. Those that survived downstream passage were potentially detected at Little Goose, Lower Monumental, Ice Harbor, McNary, John Day, and Bonneville Dams.

To be detected passing a dam, a PIT-tagged fish must enter the juvenile fish bypass system while flumes containing the PIT-tag detection systems are watered up (e.g., Prentice et al. 1990b). However, at dams along the Snake and Columbia Rivers, these flumes were dewatered seasonally during our study. This prohibited the detection of study fish that passed the dams during late fall and winter.

The PIT-tag detection systems were dewatered on the following dates and locations:

- Lower Granite Dam from 1 November 2005 to 25 March 2006
- Little Goose Dam from 1 November 2005 to 1 April 2006
- Lower Monumental Dam from 1 October 2005 to 1 April 2006

Detection data collected in 2005 and 2006 were downloaded from the PIT-tag Information System (PTAGIS), a regional database operated and maintained by the Pacific States Marine Fisheries Commission (PSMFC 1996).

Downstream Recapture of Juveniles

We used the separation-by-code systems at Lower Granite and Bonneville Dams (e.g., Downing et al. 2001) to recapture a randomly designated sample of the PIT-tagged natural, surrogate, and production subyearlings in 2005. We also compiled PIT-tag recapture records for fish that were sampled by hook and line by the Idaho Fishery Resource Office in Lower Granite Reservoir during fall 2005. The separation-by-code systems at Lower Granite and Bonneville dams were also re-programmed in 2006 to

recapture every fish from the 2005 tagging. Recaptured fish were measured (FL, mm) and weighed (wet weight, g) to evaluate size during seaward migration.

Data Analyses

We conducted data analyses and presented results in four ways. First, we summarized tagging and release results. Second, we pooled the data on Snake and Clearwater River natural subyearlings to depict passage timing at Lower Granite, Little Goose, and Lower Monumental Dams for the natural population. We did the same for the Snake and Clearwater River surrogate subyearlings surrogates.

We did not make statistical comparisons at the population level; however, the third way we analyzed data and presented results was by comparing post-release attributes among Snake River natural, surrogate, and production subyearlings. Fourth, we compared post-release attributes among Clearwater River natural, surrogate, and production subyearlings. All statistical comparisons were made separately by dam ($\alpha = 0.05$) with two exceptions: travel time and joint probability of active migration and survival were estimated and compared among the three groups of subyearlings only at Lower Monumental Dam.

Fish were not tagged in proportion to their redd production in the Snake and Clearwater River basins (i.e., 70% Snake to 30% Clearwater). Thus, direct pooling of data would have put disproportionate weight on the passage timing of Snake River fish. To adjust for this discrepancy, daily detection data of fish from the Clearwater River were expanded so that data from these fish would carry 30% of weight in the analysis. Based on the 70:30 ratio vs. the actual proportion tagged, we calculated a weighting factor of 2.1 to expand daily detection numbers of natural Clearwater River fish. For example, if 1 natural Clearwater River fish was detected on 1 September, this detection was expanded to 2.1. Similarly, an expansion factor of 1.2 was calculated and applied to daily detection data of Clearwater River surrogate subyearlings.

Passage Distribution, Timing, and Exposure to Spill

Analyses of passage timing at dams, level of exposure to spill, and travel time to Lower Monumental Dam were based upon estimated daily passage distributions at the dams. We estimated the number of fish from a PIT-tag group that passed a dam on a particular day as the number of detections from that group on that day (or the expanded number in the instance of the Clearwater River fish during population level analyses) divided by the estimated proportion of fish detected passing that day. The estimated proportion of fish passing on a given day was calculated using the methods of Sandford and Smith (2002). We used the estimated daily passage distributions as data in the statistical tests. For the sake of brevity, we do not reference these numbers as being estimates hereafter.

We used a three-sample Kolmogorov-Smirnov test (Kiefer 1959) to test for differences among cumulative passage distributions of natural, surrogate, and production subyearlings in 2005 (i.e., subyearling migrants only). A two-sample Kolmogorov-Smirnov test was used to evaluate pair-wise differences in cumulative passage distributions between each pair of groups. We reported Kolmogorov-Smirnov D_{\max} values in percentage points, which were calculated as the maximum daily difference in cumulative passage distributions between natural and surrogate subyearlings and between natural and production subyearlings.

We calculated the monthly percentage of each group of subyearlings that passed each dam by dividing monthly passage by total passage in 2005 and multiplying by 100. We ran a 3×5 chi-square analyses to determine if there was a global difference in monthly passage among the three groups of subyearlings. Next, we identified the month of peak passage for natural subyearlings and used simple chi-square tests to compare passage during this month between all pairs of groups.

For each of the three groups of subyearlings, we also calculated the percentage of total detections (i.e., 2005 and 2006 combined) made in 2006. This percentage provided an index of the relative proportion of reservoir-type juveniles in each group, noting that PIT-tag detection systems were dewatered at the dams from late fall through winter and therefore some passage went undetected. We used a three-way chi-square analyses to determine if there was a global difference between groups in the percentage of fish that passed in 2006. We then used simple chi-square analyses to make pair-wise comparisons of this percentage between all pairs of groups.

Summer spill was implemented at Lower Granite, Little Goose, and Lower Monumental Dams from 20 June to 31 August 2005. We used 2005 passage distributions to estimate the percentage of each group exposed to summer spill. For statistical tests, we transformed these percentages to meet normality assumptions. Based on residual plots, we selected an arcsine transformation for Snake River data and a natural logarithm for Clearwater River data. We then used a two-way analysis of variance (release group and dam) to test for differences in the level of exposure to spill. We used Fisher's protected least significant difference (LSD) test to evaluate pair-wise differences in level of exposure to spill between all pairs of groups.

Travel Time to Lower Monumental Dam

For each PIT-tagged subyearling detected at Lower Monumental Dam, we calculated travel time as the number of days that elapsed between release and detection. Then, for each detection date at Lower Monumental Dam, we calculated the mean travel time of all fish detected that day from each release group. Finally, average travel time for all fish from a group was estimated as the weighted mean of estimates for each detection date, with the number of subyearlings estimated to have passed Lower Monumental Dam on that date as the weight. We used a one-way analysis of variance to test for differences in weighted mean travel time to Lower Monumental Dam among natural, surrogate, and production subyearlings. We used Fisher's protected LSD test to evaluate pair-wise differences in weighted mean travel time between two release groups.

Size During Migration

We used data collected on fish recaptured at Lower Granite Dam, Bonneville Dam, and by hook and line sampling in Lower Granite Reservoir to characterized size during seaward migration as mean fork length (mm), mean weight (g) and mean condition factor K (weight divided by the cube of fork length multiplied by 10^5). Sample sizes were too small and unbalanced to conduct statistical analyses because spill decreased the number of PIT-tagged subyearlings that were susceptible to diversion and recapture.

Joint Probability of Migration and Survival

Because of the reservoir-type juvenile life history, detection data did not always conform to the classic single-release recapture model described by Cormack (1964) and Skalski et al. (1998). Lowther and Skalski (1998) attempted to develop a model to deal with data of this nature. However, dewatering of PIT-tag detection systems at the dams during late fall and winter resulted in violation of a critical assumption of both the single-release and Lowther and Skalski models (1998).

One option for dealing with this situation was to use only detections of subyearlings that occurred during the year of release (i.e., year t). This results in data more likely to fit assumptions of the single-release model, but requires a reinterpretation of model parameters. By ignoring information collected on reservoir-type juveniles in year $t+1$, there is no distinction in the data between cessation of active migration and mortality during the year of release. Consequently, the parameter that is usually interpreted as the probability of survival must instead be interpreted as the joint probability of survival and active migration.

Natural fall Chinook salmon from the Snake River upstream from its confluence with the Salmon River rarely exhibit the reservoir-type juvenile life history (2% and less; Connor et al. 2002). Thus, we can assume that few of these fish pass dams undetected from late fall to winter, when the PIT-tag detection systems are dewatered. Ignoring detections of reservoir-type juveniles year $t+1$ after the PIT-tag detection systems are watered up, a typical single-release model "survival" estimate to the tailrace of Lower Granite Dam for upper Snake River reach fish might be 69%.

In reality, this estimate is the product of the probability of migrating as a subyearling smolt and passing the Lower Granite Dam when the PIT-tag detection system is watered up (e.g., 98%) and the probability of surviving to the tailrace of Lower Granite Dam as a subyearling (e.g., 70%). That is, $69\% = 98\% \times 70\%$. Thus these natural fall Chinook stocks, the estimate of the joint probability of migration and survival is only one percentage point lower than that of survival alone. Therefore, the joint estimate is a relatively unbiased measure of actual survival probability alone.

However, natural fall Chinook salmon from the Clearwater River exhibit the reservoir-type juvenile life history more frequently (e.g., 6–85%; Connor et al. 2002) than those from the Snake River upstream of the Salmon River confluence. The prevalence of late fall passage, as well as empirical observations (Tiffan and Connor 2005; B. Arnsberg, Nez Perce Tribe, unpublished data), suggest that these reservoir-type juveniles commonly pass dams undetected during the winter, when PIT tag detection systems are dewatered.

Ignoring detections of reservoir-type juveniles that occur in the spring following release, a typical single-release model “survival” estimate to the tailrace of Lower Granite Dam for Clearwater fish might be 16%. Again, this quantity actually estimates the probability of migrating as a subyearling when the PIT-tag detection system is watered up (e.g., 40%) and the probability of surviving to the tailrace of Lower Granite Dam (e.g., 40%; i.e., $40\% \times 40\% = 16\%$). In this case, the joint estimate of migration and survival is 24 percentage points lower than that of survival alone.

In the first step of data analysis, we divided each release group of PIT-tagged natural subyearlings into two intra-annual groups referred to as “cohorts” (Connor et al. 2003). For Snake and Clearwater River surrogate subyearlings, we divided the data into intra-annual release groups based on week of tagging ($n = 2$ in the Snake River; $n = 3$ in the Clearwater River). Production fish were kept in their original release groups by location ($n = 4$ in the Snake River; $n = 1$ release in the Clearwater River). We calculated SEs as described by Zar (1984) with the exception of the Clearwater River production subyearlings, in which case we used the methods described by Cormack (1964) and Skalski et al. (1998).

To test for differences among survival estimates for natural, surrogate, and production subyearlings, we square-root transformed the joint probability estimates for each group, then used one-way analysis of variance, with release group as the factor. We used Fisher's protected LSD test to evaluate differences in the estimates between two release groups.

Paired Comparisons of Attributes

The preceding methods described 15 potential comparisons between natural and surrogate subyearlings and 15 between natural and production subyearlings. Of the 30 comparisons, 28 potentially involved pair-wise comparisons to test null hypotheses. We finished the Snake River and Clearwater River analyses with river-specific summaries. We calculated a standardized index of attribute similarity between natural subyearlings and each of the two groups of hatchery subyearlings. We also tabulated the outcomes of hypothesis tests (i.e., yes, rejected H_0 ; no, failed to reject H_0).

To calculate each index, the higher value of an attribute was always divided by its lower value. For example, if travel time to Lower Monumental Dam was 41 d for natural subyearlings and 45 d for surrogates, the index for surrogates would be 1.1 (45/41). Likewise, if travel time was 41 d for natural subyearlings and 20 d for production subyearlings the index for production subyearlings would be 2.0 (41/20). From this

example, we would conclude there was a 1.1-fold difference between the mean travel times of natural and surrogate subyearlings and a twofold difference between the mean travel times of natural and production subyearlings.

Values used to calculate the indices varied by attribute. In the instance of cumulative passage, we used the cumulative percent passage values observed at D_{\max} . For peak monthly passage, we used percentages of groups that passed during the peak month of passage observed for natural subyearlings. For comparing passage in 2006, we used the percentages of total passage observed in 2006 (i.e., 2005 and 2006 combined). For exposure to spill, we calculated indices from the percentages of each group that passed when spill was implemented in 2005. For travel time, we used values as shown in the example above for Lower Granite Dam. We calculated indices for comparing size during migration using measurements taken at Lower Granite Dam (the only dam where adequate sample sizes could be collected). Finally, for the joint probability of active migration and survival to the tailrace of Lower Monumental Dam, we used means of the combined probabilities.

RESULTS

Fish Collection, Tagging, and Release

The number of subyearlings PIT tagged and released into the Snake River was lowest for natural fish and highest for surrogates (Table 1). Natural subyearlings were released in the Snake River over a more protracted period than surrogate or production subyearlings. Tagged natural subyearlings averaged 8 mm smaller in fork length than surrogate subyearlings and 12–19 mm smaller than production subyearlings. Snake River natural and production subyearlings were more robustly shaped at time of tagging (i.e., greater condition factor K) than Snake River surrogates.

Table 1. The number (N), range of release dates, mean fork length (mm \pm SD), mean weight (g \pm SD), and condition factor ($K \pm$ SD) of PIT-tagged Snake River and Clearwater River natural, surrogate, and production subyearlings released in 2005.

Release group	N	Release dates	Fork length (mm)	Weight (g)	Condition factor (K)
<i>Snake River</i>					
Natural	9,300	14 April–5 July	68 +7	3.6 +1.5	1.10 +0.09
Surrogate	124,447	16 May–27 May	76 +8	4.0 +1.3	0.95 +0.0
Production					
Hells Canyon Dam	9,972	28 April	80 +8		
Pittsburg Landing	2,492	26 May	86 +7	7.1 +1.6	1.14 +0.08
Captain John Rapids	3,494	26 May–30 May	87 +10	7.0 +2.4	1.10 +0.09
Couse Creek	3,465	26 May	86 +8	7.3 +2.3	1.15 +0.09
<i>Clearwater River</i>					
Natural	1,875	03 May–03 Aug	72 +9	4.4 +0.1	1.13 +0.10
Surrogate	45,790	21 Jun–08 July	73 +9	4.1 +1.5	0.95 +0.13
Production					
Big Canyon Creek	2,498	31 May	90 +8	8.3 +2.0	1.10 +0.10

The number of subyearlings PIT tagged and released into the Clearwater River was lowest for natural fish and highest for surrogate subyearlings (Table 1). Natural subyearlings were released in the Clearwater River over a more protracted period than surrogate or production subyearlings. Natural subyearlings averaged 1 mm smaller in fork length than surrogate subyearlings and 18 mm smaller than production subyearlings. Among Clearwater River releases, natural and production subyearlings were more robustly shaped than surrogate subyearlings.

Population Level Passage

Passage at Lower Granite Dam by populations of natural and surrogate subyearlings was a protracted event in 2005 (Figure 2). Passage of both natural and surrogate subyearling populations at Lower Granite Dam peaked on 18 June. In 2005, passage at the dam of natural and surrogate subyearling populations was 95% complete on 10 and 14 August, respectively. An increase in passage of both natural and surrogate subyearling populations began on 8 October and continued until 1 November, when the PIT-tag detection system at the dam was dewatered.

Reservoir-type juveniles detected at Lower Granite Dam after operation of the PIT-tag monitoring system had resumed made up 2.3 and 1.3% of total passage by natural and surrogate subyearlings, respectively (Figure 2). Passage of natural reservoir-type juveniles was first documented 3 d after the PIT-tag detection system was watered up, and passage of surrogate reservoir-type juveniles was first documented on the day of water up (25 March 2006). At Lower Granite Dam, final detections of reservoir-type natural and surrogate juveniles occurred on 19 April and 12 May 2006, respectively.

Passage at Little Goose Dam by populations of natural and surrogate subyearlings was also a protracted event in 2005 (Figure 3). Passage of both natural and surrogate subyearling populations peaked at Little Goose Dam on 1 July. In 2005, passage at Little Goose Dam of natural and surrogate subyearling populations was 95% complete on 17 and 19 July, respectively. These dates of 95% completion at Little Goose Dam were earlier than at Lower Granite Dam. This anomaly was likely the result of fish ceasing migration or dying after passing Lower Granite Dam. An increase in passage of the population of surrogate subyearlings began on 8 October and continued until the PIT-tag detection system was dewatered at Little Goose Dam on 1 November 2005. Passage of the population of natural subyearlings did not increase in October.

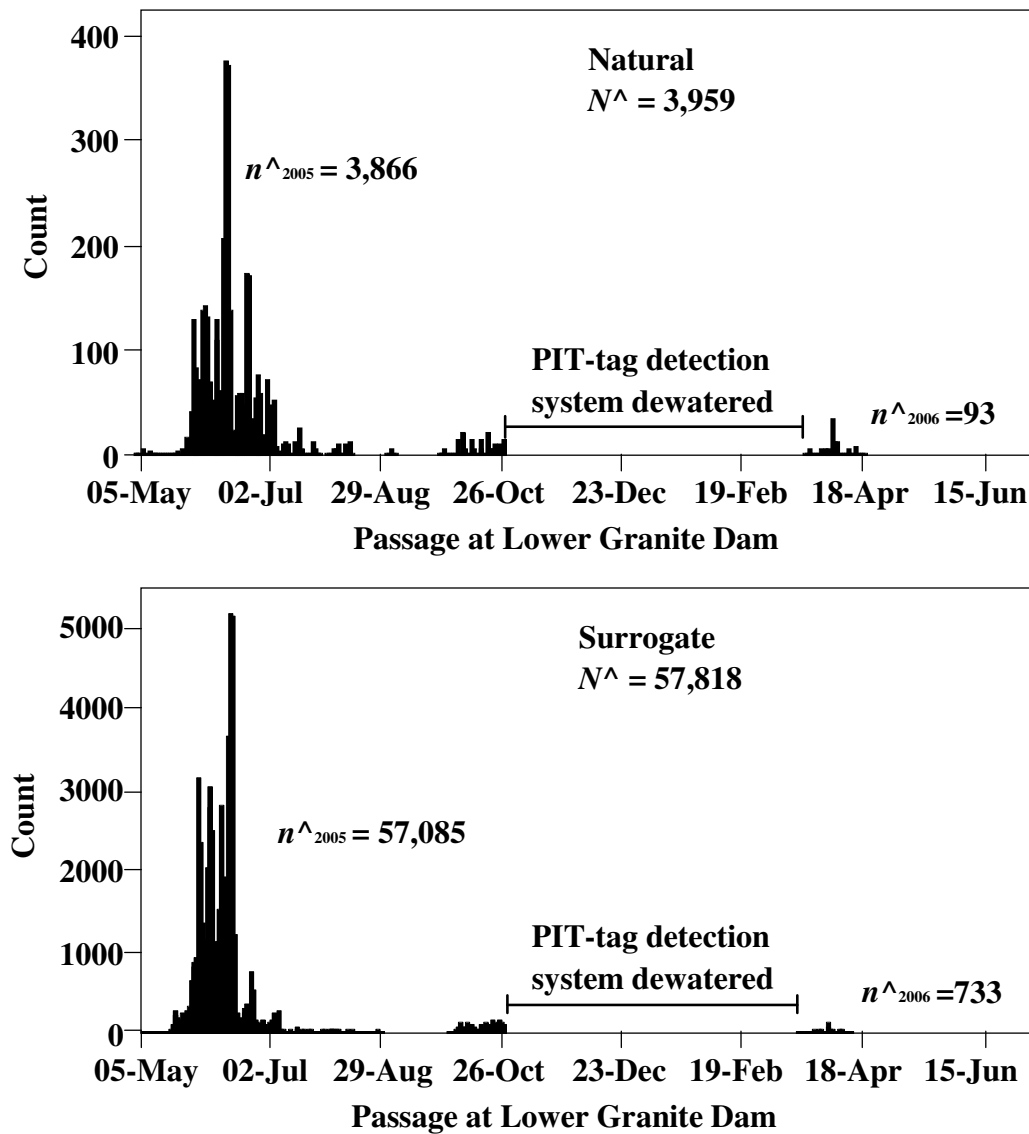


Figure 2. Estimated passage distributions at Lower Granite Dam in 2005 and 2006 for the population of natural (top panel) and surrogate (bottom panel) fall Chinook salmon subyearlings captured, PIT-tagged and released into the Snake and Clearwater rivers in 2005. Daily detection data were expanded based on detection probability and summed for 2005 and 2006 pooled (N^{\wedge}) and for 2005 (n^{\wedge}_{2005}) and 2006 (n^{\wedge}_{2006}).

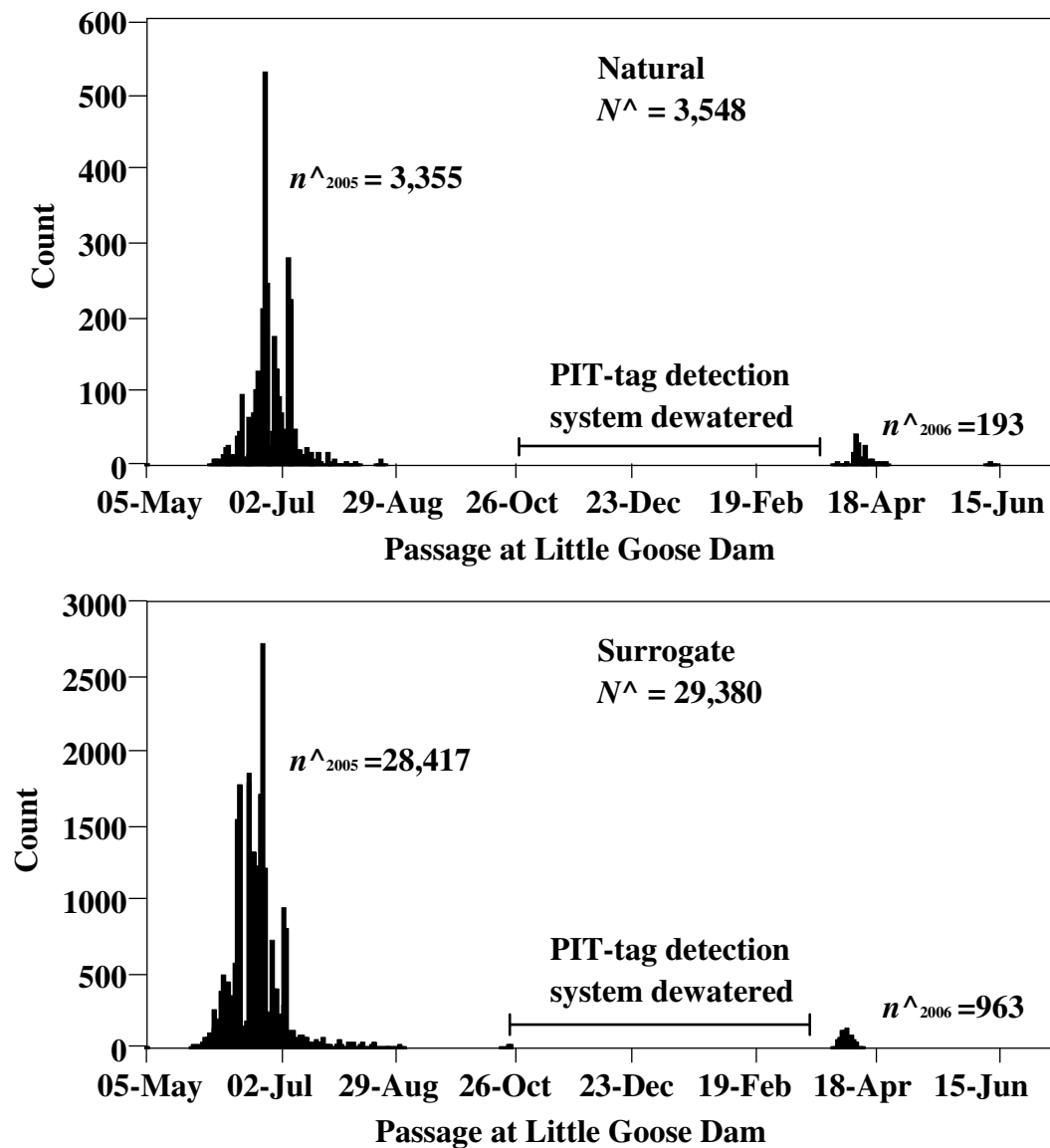


Figure 3. Estimated passage distributions at Little Goose Dam in 2005 and 2006 for the population of natural (top panel) and surrogate (bottom panel) fall Chinook salmon subyearlings captured, PIT-tagged and released into the Snake and Clearwater rivers in 2005. Daily detection data were expanded based on detection probability and summed for 2005 and 2006 pooled (N^{\wedge}) and for 2005 (n^{\wedge}_{2005}) and 2006 (n^{\wedge}_{2006}).

Reservoir-type juveniles detected at Little Goose Dam after operation of the PIT-tag monitoring system had resumed made up 5.4 and 3.3% of total passage by natural and surrogate subyearlings, respectively (Figure 3). Passage of both natural and surrogate reservoir-type juveniles was first documented 1 d after the PIT-tag detection system was watered up on 1 April. At Little Goose Dam, final detections of reservoir-type natural and surrogate juveniles occurred on 25 April and 17 May 2006, respectively.

Passage at Lower Monumental Dam by natural and surrogate subyearling populations was also a protracted event in 2005 (Figure 4). Passage at Lower Monumental Dam of the populations of natural and surrogate subyearlings peaked on 30 and 29 June, respectively. Passage of the populations of natural and surrogate subyearlings in 2005 was 95% complete at Lower Monumental Dam on 24 and 22 July, respectively. This was earlier than at Lower Granite Dam, but later than at Little Goose Dam. Perhaps more subyearlings in the population ceased migration or died after passing Lower Granite Dam than after passing Little Goose Dam. Passage of natural and surrogate subyearling populations did not increase in October.

Reservoir-type juveniles detected at Lower Monumental Dam after operation of the PIT-tag monitoring system resumed made up 7.9 and 5.1% of total passage by natural and surrogate subyearlings, respectively (Figure 4). Natural reservoir-type juveniles began passing the day after the PIT-tag detection system was watered up on 1 April. Passage of surrogate reservoir-type juveniles began on 1 April. At Little Goose Dam final detections of reservoir-type natural and surrogate juveniles occurred on 25 April and 17 May 2006, respectively.

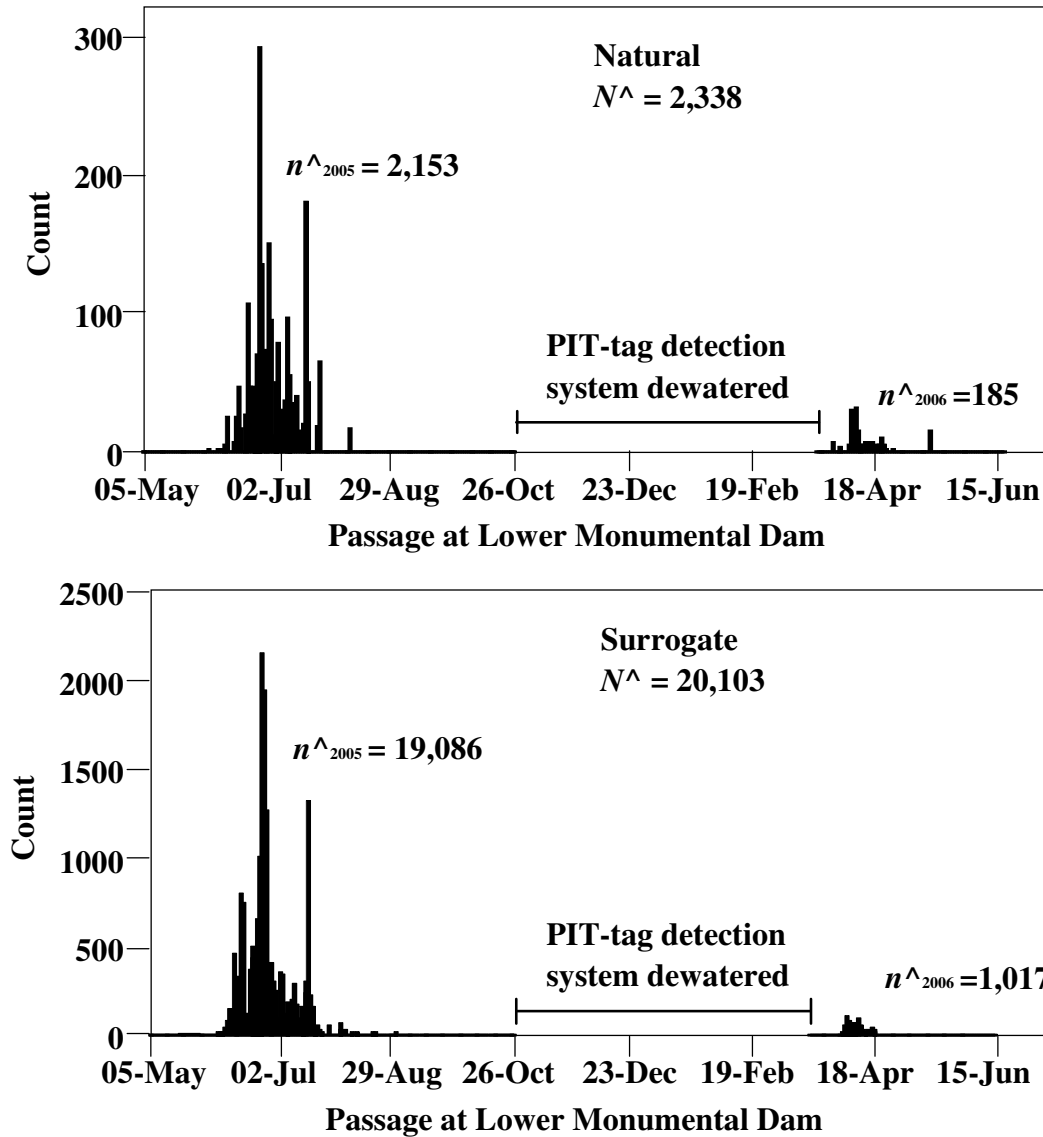


Figure 4. Estimated passage distributions Passage timing at Lower Monumental Dam in 2005 and 2006 for the population of natural (top panel) and surrogate (bottom panel) fall Chinook salmon subyearlings captured, PIT-tagged and released into the Snake and Clearwater rivers in 2005. Daily detection data were expanded based on detection probability and summed for 2005 and 2006 pooled (N^{\wedge}) and for 2005 (n^{\wedge}_{2005}) and 2006 separately (n^{\wedge}_{2006}).

Snake River

Passage Timing and Distribution

For Snake River subyearlings, production fish passed Lower Granite, Little Goose, and Lower Monumental Dams earlier in 2005 than surrogates, which in turn passed earlier than natural fish (Figure 5). Cumulative percent passage at these dams varied significantly among the three groups and between all pairs of groups (all global and pair-wise P values < 0.0001). June passage of production subyearlings progressed at a faster rate than that of surrogates, which in turn progressed at a faster rate than that of natural subyearlings.

Peak monthly passage at Lower Granite Dam in 2005 was in June for Snake River natural subyearlings, when 84% passed (Figure 6) compared with 89% of surrogate and 50% of production subyearlings. At Little Goose Dam in 2005, peak monthly passage for Snake River natural subyearlings was in July, when 67% of these fish passed compared with 32% of surrogates and 0.3% of production subyearlings. Peak monthly passage of natural subyearlings at Lower Monumental Dam in 2005 was in July when 64% passed the dam compared to 40% of surrogate and 2% of production subyearlings.

Monthly passage at Lower Granite, Little Goose, and Lower Monumental Dams during 2005 varied significantly (all global P values < 0.0001) among Snake River natural, surrogate, and production subyearlings. The percentage of passage during the peak month of natural subyearling passage also varied significantly (all pair-wise P values < 0.0001) between all pairs of subyearling groups at all three dams.

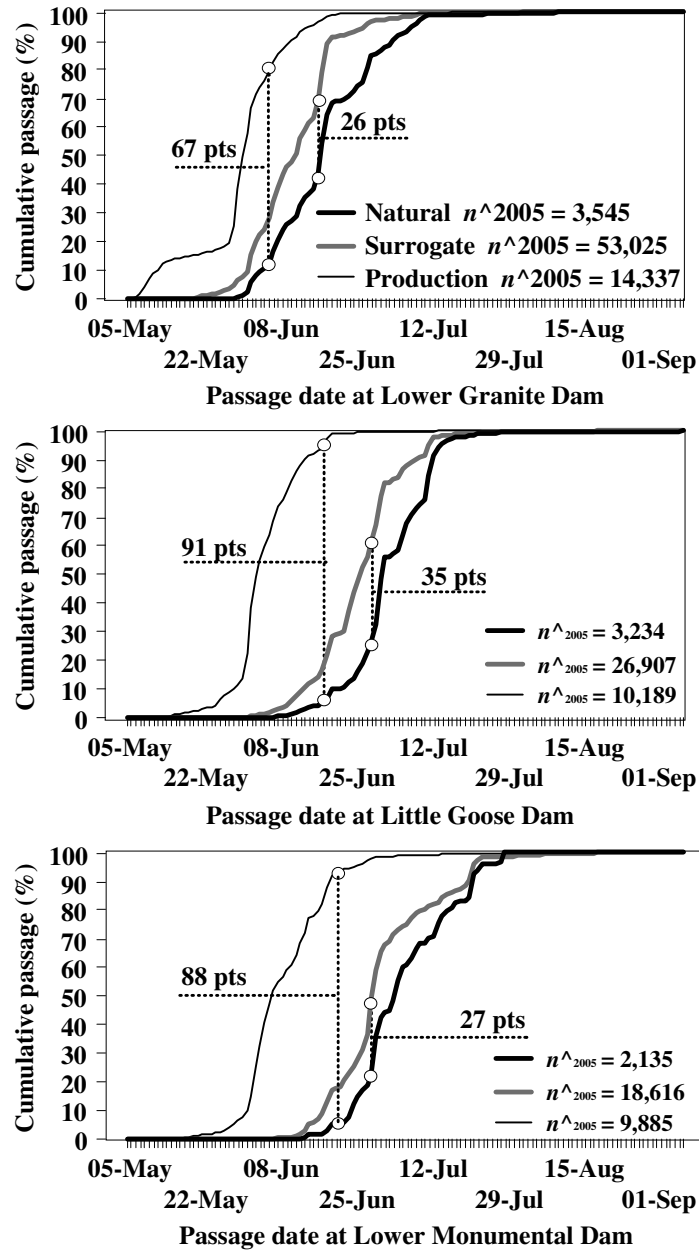


Figure 5. Estimated cumulative passage distributions at Lower Granite, Little Goose , and Lower Monumental Dams for Snake River natural, surrogate, and production fall Chinook salmon subyearlings in 2005. Percentage points (pts) and dotted arrows indicate D_{max} values calculated as the maximum daily difference between cumulative passage distributions of natural and surrogate subyearlings and between natural and production subyearlings. Estimated passage numbers (n^{\wedge}) are given beside the legend lines.

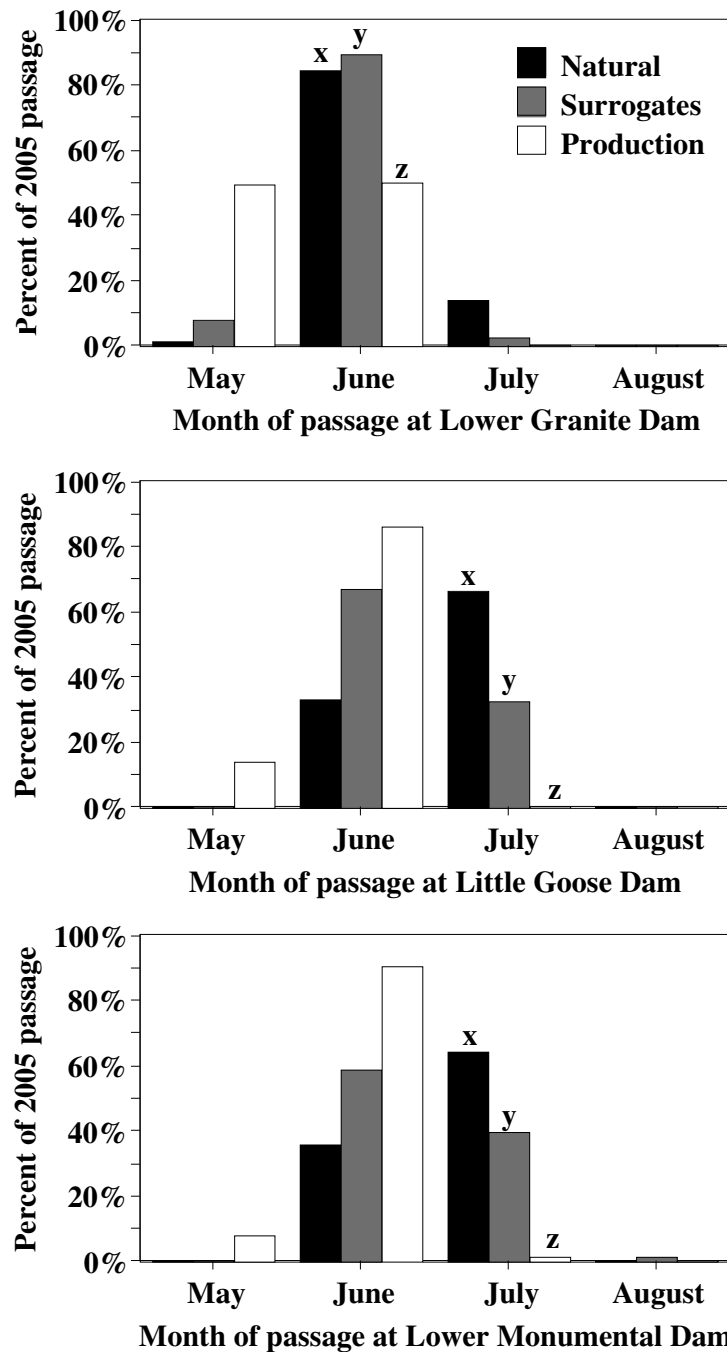


Figure 6. The percentage of the estimated number of Snake River natural, surrogate, and production subyearlings that passed Lower Granite, Little Goose, and Lower Monumental Dams during July-August 2005. The different letters over the passage bars indicate significant ($P < 0.05$) differences in passage among the three groups of subyearlings during the month of peak passage of natural subyearlings. Estimated passage numbers for 2005 are given in Figure 5.

Of the Snake River natural juveniles that passed Lower Granite Dam in 2005 and 2006 ($N = 3,551$), 0.2% exhibited a reservoir-type juvenile life history and passed in 2006 ($n_{2006} = 6$) compared to 0.04% for surrogate juveniles ($N = 53,045$; $n_{2006} = 20$). No production juveniles passed Lower Granite Dam in 2006. Of the natural juveniles that passed Little Goose Dam in 2005 and 2006 ($N = 3,251$), 0.5% passed in 2006 ($n_{2006} = 17$) compared to 0.7% for surrogate juveniles ($N = 27,087$; $n_{2006} = 180$) and 0.02% for production juveniles ($N = 10,191$; $n_{2006} = 2$). Of the natural juveniles that passed Lower Monumental Dam in 2005 and 2006 ($N = 2,161$), 1.2% passed in 2006 ($n_{2006} = 26$) compared to 0.2% for surrogate juveniles ($N = 18,644$; $n_{2006} = 28$) and 0.03% for production juveniles ($N = 9,888$; $n_{2006} = 3$). The percentages of juveniles that passed in 2006 varied significantly (all global P values < 0.0001) among the three groups of juveniles at all three dams. The percentage of natural juveniles that passed in 2006 was significantly (all pair-wise comparisons < 0.02) higher than was observed for surrogate and production subyearlings except in the case of surrogate juveniles at Little Goose Dam ($P = 0.3$).

Exposure to Summer Spill

The percentage of Snake River subyearlings exposed to summer spill at Lower Granite Dam was 35% for natural, 11% for surrogate, and 2% for production subyearlings (Figure 7). The percentage of fish exposed to summer spill at Little Goose Dam was 93% for natural, 78% for surrogate, and 3% for production subyearlings. The percentage of fish exposed to summer spill at Lower Monumental Dam was 97% for natural, 87% for surrogate, and 12% for production subyearlings. The percentage of Snake River subyearlings exposed to summer spill varied significantly among the three release groups (global $P = 0.04$) but not among the three dams (global $P = 0.08$). There was no significant difference in the percentage of fish exposed to summer spill between natural and surrogate subyearlings (pair-wise $P = 0.30$), whereas a significantly lower percentage of production subyearlings were exposed to summer spill than natural (pair-wise $P = 0.02$) and surrogate subyearlings (pair-wise $P = 0.05$).

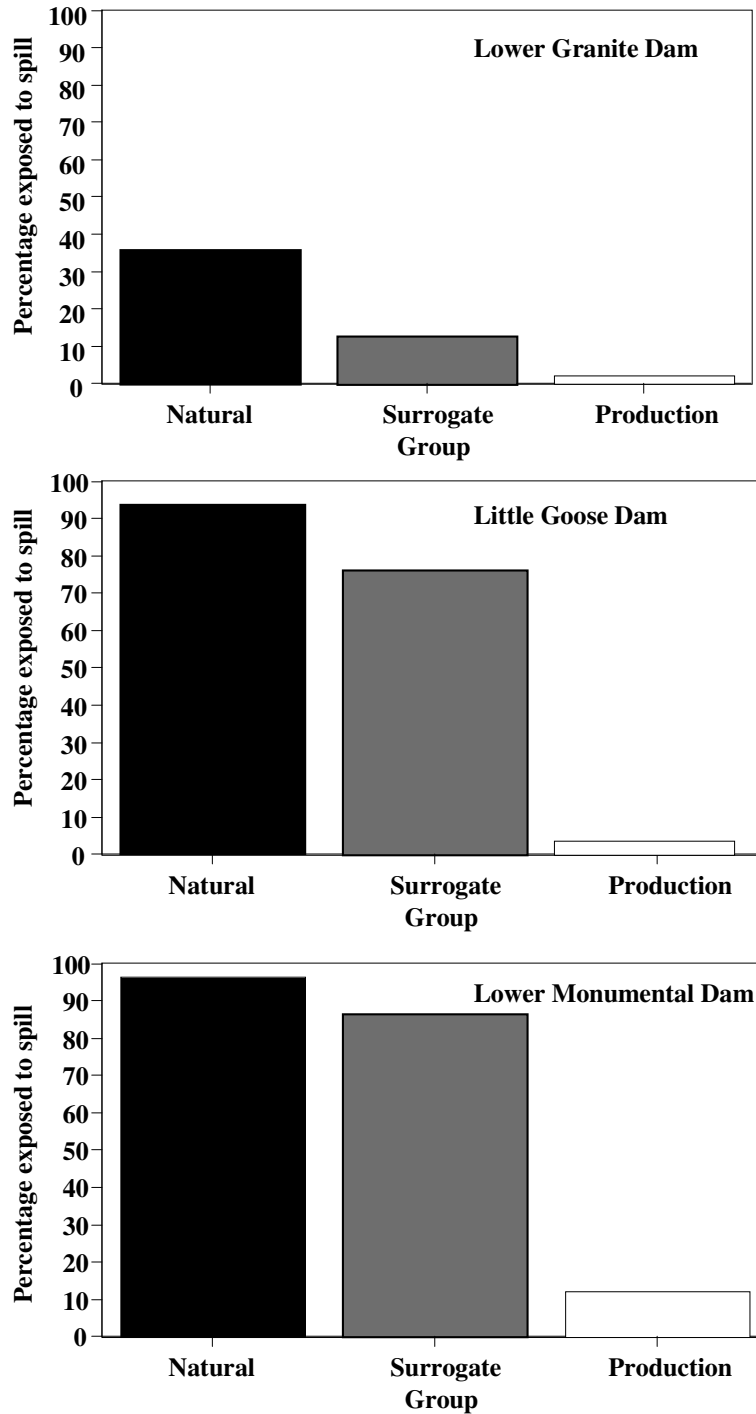


Figure 7. Estimated percentages of Snake River natural, surrogate, and production fall Chinook salmon subyearlings that migrated and were exposed to spill in 2005 at Lower Granite (top panel), Little Goose (middle panel), and Lower Monumental (bottom panel) Dams. Estimated passage numbers for 2005 are given in Figure 5.

Travel Time to Lower Monumental Dam

Weighted mean travel time (\pm SE) to Lower Monumental Dam for Snake River fish in 2005 was 45 ± 0.2 d for natural subyearlings ($n^{2005} = 2,135$), 41 ± 0.1 d for surrogate subyearlings ($n^{2005} = 18,616$), and 28 ± 0.1 d for production subyearlings ($n^{2005} = 9,885$). Weighted mean travel time varied significantly among these three release groups ($P < 0.0001$) in 2005 and all pair-wise comparisons were significant (all P values < 0.0001).

Size During Migration

For Snake River fish recaptured at Lower Granite Dam in 2005, natural subyearlings averaged 9 mm larger in fork length than surrogates and 9 mm smaller in fork length than production subyearlings (Table 2). All subyearlings were robustly shaped (i.e., $K > 1.0$) when recaptured at Lower Granite Dam, but condition factor was higher for natural and surrogate subyearlings than it was for production subyearlings.

Table 2. Mean fork length (mm \pm SD), weight (g \pm SD), and condition factor ($K \pm$ SD) of PIT-tagged Snake River natural, surrogate, and production subyearlings released in 2005 and recaptured at Lower Granite and Bonneville Dams in 2005 and 2006.

Recapture dam	Group	N	Recapture dates		Fork length		Condition factor (K)
			Min	Max	(mm)	Weight (g)	
2005							
Lower Granite	Natural	23	02-Jun	07-Jul	91 +10	8.4 +3.0	1.06 +0.09
	Surrogate	39	26-May	20-Jun	82 +10	6.0 +2.0	1.05 +0.10
	Production	299	31-May	24-Jun	100 +9	10.5 +2.9	1.02 +0.08
Bonneville	Natural	8	06-Jul	20-Jul	118 +6	16.9 +3.4	1.02 +0.08
	Surrogate	69	06-Jul	03-Aug	112 +8	15.7 +5.0	1.08 +0.10
2006							
Lower Granite	Surrogate	1	17-Apr	17-Apr	218	127.7	1.23
Bonneville	Surrogate	2	18-Apr	18-Apr	227 +39	130.6 +72	1.06 +0.07

For Snake River fish recaptured at Bonneville Dam in 2005, natural subyearlings averaged 6 mm larger in fork length than surrogates (Table 2). Natural subyearlings maintained a robust body shape during downstream passage, but in 2005, average condition factor for natural subyearlings recaptured at Bonneville Dam was lower than for those recaptured at Lower Granite Dam. Average condition factor for surrogates recaptured at Bonneville Dam was higher than for those recaptured at Lower Granite Dam.

A few Snake River natural and surrogate fall Chinook that had been released as subyearlings in 2005 were collected at Lower Granite and Bonneville Dams in 2006 (Table 2). These yearlings were large in fork length and had a robust body shape.

Joint Probability of Migration and Survival.

For Snake River fish, the mean joint probability of active migration and survival from release to the tailrace of Lower Monumental Dam (\pm SE) was $23.4 \pm 6.5\%$ for natural subyearlings ($N = 2$ intra-annual release groups), $16.1 \pm 0.1\%$ for surrogates ($N = 2$ intra-annual release groups), and $55.0 \pm 3.8\%$ for production subyearlings ($N = 4$ intra-annual release groups). The mean joint probability of active migration and survival from release to the tailrace of Lower Monumental Dam varied significantly among the three Snake River release groups ($P = 0.002$); however, it was not significantly different between natural and surrogate subyearling groups ($P = 2$). In contrast, mean joint probability of migration and survival to Lower Monumental Dam was significantly higher for production than for natural ($P = 0.004$) and surrogate subyearling groups ($P = 0.001$).

Overall Comparison of Attributes

For Snake River fish, the similarity was greater between natural and surrogate subyearlings than between natural and production subyearlings with respect to 14 of the 15 attributes studied (Table 3). On average, there was a 2.3-fold difference in attributes between natural and surrogate subyearlings, compared to a 31.3-fold difference in attributes between natural and production subyearlings. The null hypothesis rejection rate was 57% for tests between natural and surrogate subyearlings compared to 100% for tests between natural and production subyearlings.

Table 3. Similarity indices (higher value divided by lower value of the attribute) for each comparison between Snake River fish: natural (Ns) vs. surrogate (S) subyearlings and natural (Np) vs. production subyearlings (P). An index value of 1.0 indicates no difference, while a value of 2.0 indicates a two-fold difference, etc. Results of hypothesis tests conducted between natural vs. surrogate subyearlings and between natural vs. production subyearlings are also given (yes, rejected H_0 ; no, failed to reject H_0).

Attribute	Ns	Np	S	P	Similarity indices		H ₀ rejected	
					S	P	S	P
Lower Granite Dam								
Cumulative passage	0.443	0.129	0.698	0.797	1.6	6.2	Yes	Yes
Peak monthly passage	0.844	0.844	0.891	0.501	1.1	1.7	Yes	Yes
Passage in 2006	0.002	0.002	0.0004	0.000	4.5		Yes	Yes
Exposure to spill	0.353	0.353	0.111	0.016	3.2	21.9	No	Yes
Migrant size (mm)	91	91	82	100	1.1	1.1	N/A	N/A
Little Goose Dam								
Cumulative passage	0.263	0.070	0.609	0.975	2.3	13.9	Yes	Yes
Peak monthly passage	0.666	0.666	0.324	0.003	2.1	222.0	No	Yes
Passage in 2006	0.005	0.005	0.007	0.0002	1.3	26.8	Yes	Yes
Exposure to spill	0.929	0.929	0.777	0.025	1.2	36.6	No	Yes
Lower Monumental Dam								
Cumulative passage	0.223	0.064	0.485	0.944	2.2	14.7	Yes	Yes
Peak monthly passage	0.640	0.640	0.398	0.015	1.6	42.7	Yes	Yes
Passage in 2006	0.012	0.012	0.002	0.0003	8.1	40.1	Yes	Yes
Exposure to spill	0.967	0.967	0.866	0.123	1.1	7.9	No	Yes
Travel time	45	45	41	28	1.1	1.6	No	Yes
Migration/survival	0.234	0.234	0.161	0.550	1.5	2.4	No	Yes
Overall means and percentages					2.3 (14)	31.3 (14)	57%	100%

Clearwater River

Passage Timing and Distribution

For Clearwater River fish, production subyearlings passed Lower Granite and Little Goose Dams in early summer 2005, whereas passage of natural and surrogate subyearlings extended into fall 2005 (Figures 8 and 9). Cumulative passage at Lower Monumental Dam was not statistically analyzed because of the limited data for natural subyearlings (Figure 10).

The maximum difference between cumulative passage at Lower Granite Dam of Clearwater River natural and surrogate subyearlings was on 23 July, when 36% of natural subyearlings had passed compared to 14% of surrogates (D_{\max} , 22 points). The maximum difference between cumulative passage at Lower Granite Dam of natural and production subyearlings was on 28 June, when 15% of natural subyearlings had passed compared to 97% of production subyearlings (D_{\max} , 82 points). The maximum difference between cumulative passage at Little Goose Dam of natural and surrogate subyearlings was on 4 August, when 78% of natural subyearlings had passed compared to 57% of surrogate subyearlings (D_{\max} , 21 points). The maximum difference between cumulative passage at Little Goose Dam of natural and production subyearlings was on 30 June when 8% of natural subyearlings had passed compared to 95% of production subyearlings (D_{\max} , 87 points).

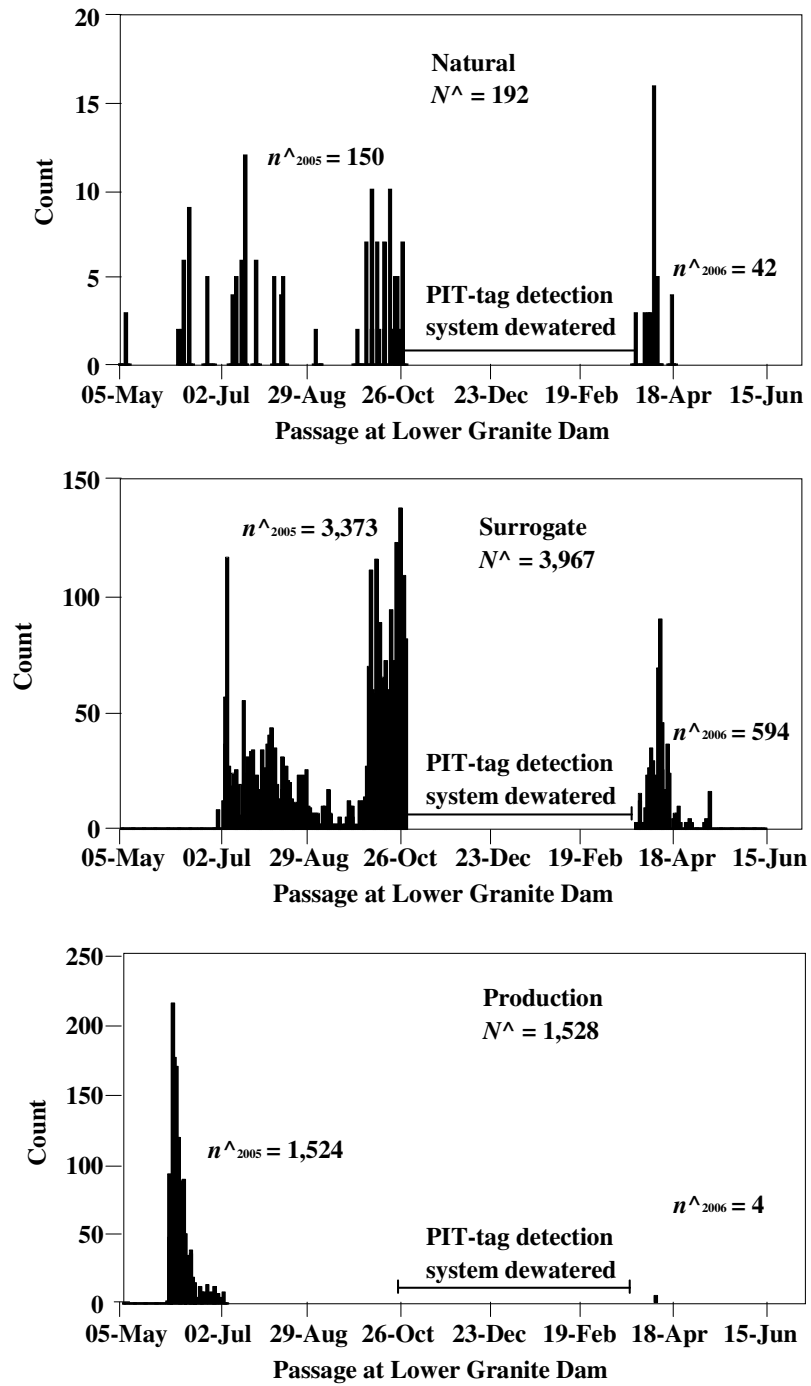


Figure 8. Estimated passage distributions at Lower Granite Dam in 2005 and 2006 for Clearwater River natural (top panel), surrogate (middle panel), and production (bottom panel) fall Chinook salmon subyearlings. Daily detection data were expanded based on detection probability and summed for 2005 and 2006 pooled (N^{\wedge}) and for 2005 (n^{\wedge}_{2005}) and 2006 (n^{\wedge}_{2006}).

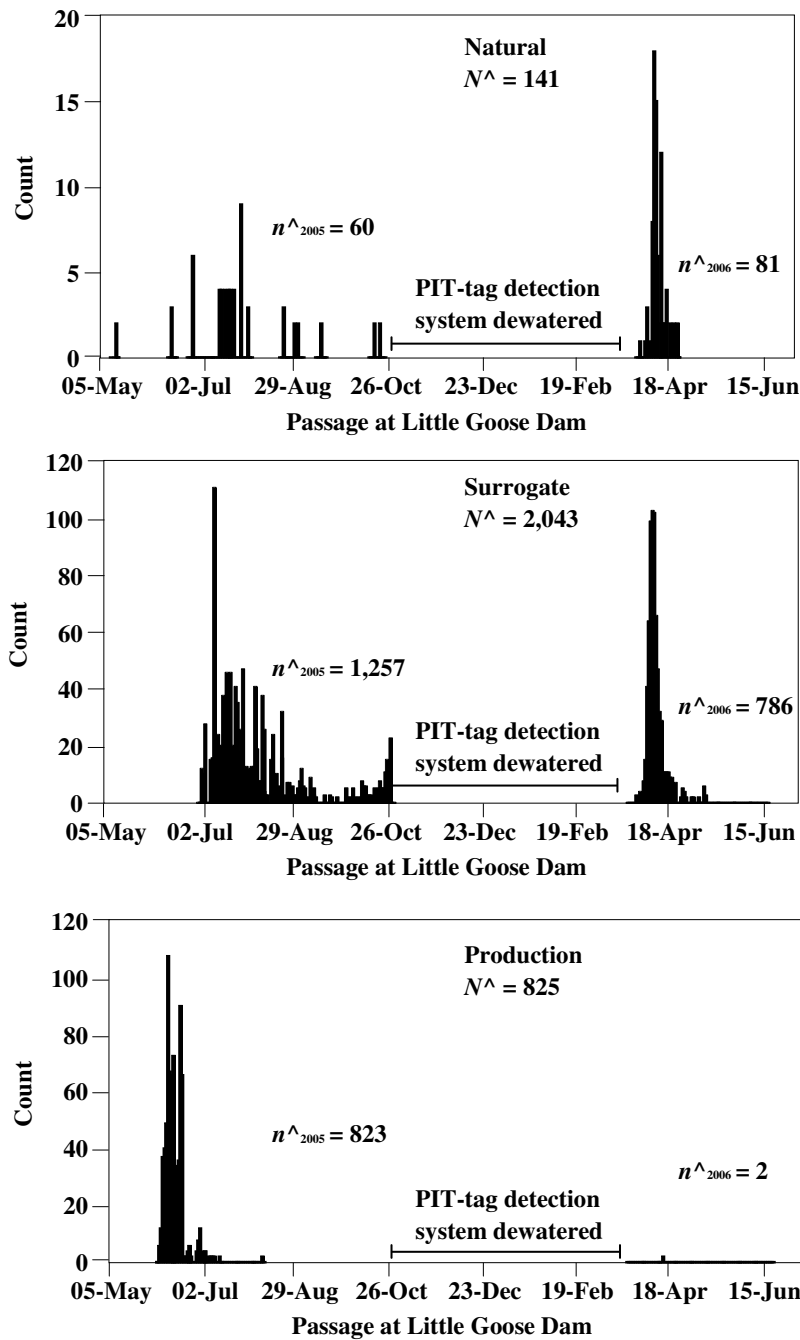


Figure 9. Estimated passage distributions at Little Goose Dam in 2005 and 2006 for Clearwater River natural (top panel), surrogate (middle panel), and production (bottom panel) fall Chinook salmon subyearlings. Daily detection data were expanded based on detection probability and summed for 2005 and 2006 pooled (N^{\wedge}) and for 2005 (n^{\wedge}_{2005}) and 2006 (n^{\wedge}_{2006}).

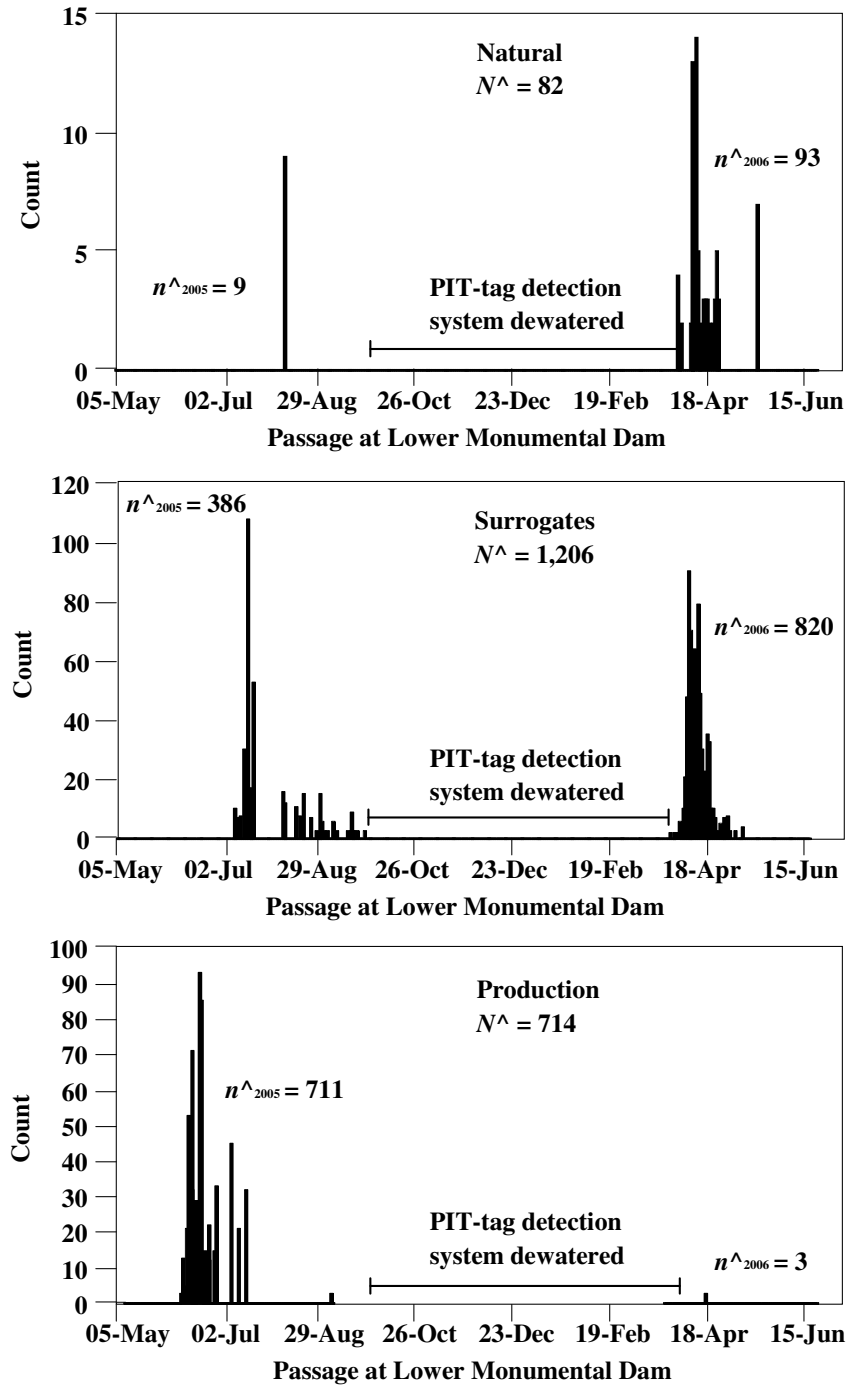


Figure 10. Estimated passage distributions at Lower Monumental Dam in 2005 and 2006 for Clearwater River natural (top panel), surrogate (middle panel), and production (bottom panel) fall Chinook salmon subyearlings. Daily detection data were expanded based on detection probability and summed for 2005 and 2006 pooled (N^{\wedge}) and for 2005 (n^{2005}) and 2006 (n^{2006}).

Passage date distributions at Lower Granite and Little Goose dams varied significantly among the three groups of subyearlings and between all pairs of groups (all global and pair-wise P values < 0.0001).

For Clearwater River fish in 2005, peak monthly passage at Lower Granite Dam was in October, when 49% of natural subyearlings passed the dam compared to 59% of surrogates and 0% of production subyearlings (Figure 11). At Little Goose Dam, peak monthly passage for natural subyearlings was in July, when 65% passed compared to 54% of surrogate and 4% of production subyearlings. Peak passage of natural and surrogate subyearlings was later at Lower Granite than at Little Goose Dam because some fish ceased migration or died after passing Lower Granite Dam.

Monthly passage at Lower Granite and Little Goose Dams during 2005 varied significantly (both global P values < 0.0001) among Clearwater River natural, surrogate, and production subyearlings. The percentage of passage during the peak month of natural subyearling passage also varied significantly (all pair-wise P values < 0.05) between all pairs of subyearling groups at Lower Granite Dam. The percentage of passage during the peak month of passage of natural subyearlings did not vary significantly ($P = 0.1$) between natural and surrogate subyearlings at Little Goose Dam, whereas passage during this period varied significantly between natural and production subyearlings ($P < 0.0001$) and surrogate and production subyearlings ($P < 0.0001$).

Of Clearwater River juveniles that passed Lower Granite Dam in 2005 and 2006, 22% of natural fish exhibited a reservoir-type life history and passed in 2006 compared to 15% of surrogates and 0.3% of production fish (Figure 8). Of juveniles that passed Little Goose Dam in 2005 and 2006, 57% of natural fish passed in 2006 compared to 39% of surrogates and 0.2% of production fish (Figure 9). Of juveniles that passed Lower Monumental Dam in 2005 and 2006 combined, 89% of natural fish passed in 2006 compared to 68% of surrogates and 0.4% of production juveniles (Figure 10).

Of the natural, surrogate, and production juveniles that passed in 2005 and 2006, the percentages that passed in 2006 varied significantly (all global P values < 0.0001) among the three groups of juveniles at all three dams. The percentage of natural fish that passed in 2006 was significantly higher at all three dams than that of surrogate and production fish (all pair-wise comparisons $P \leq 0.0004$).

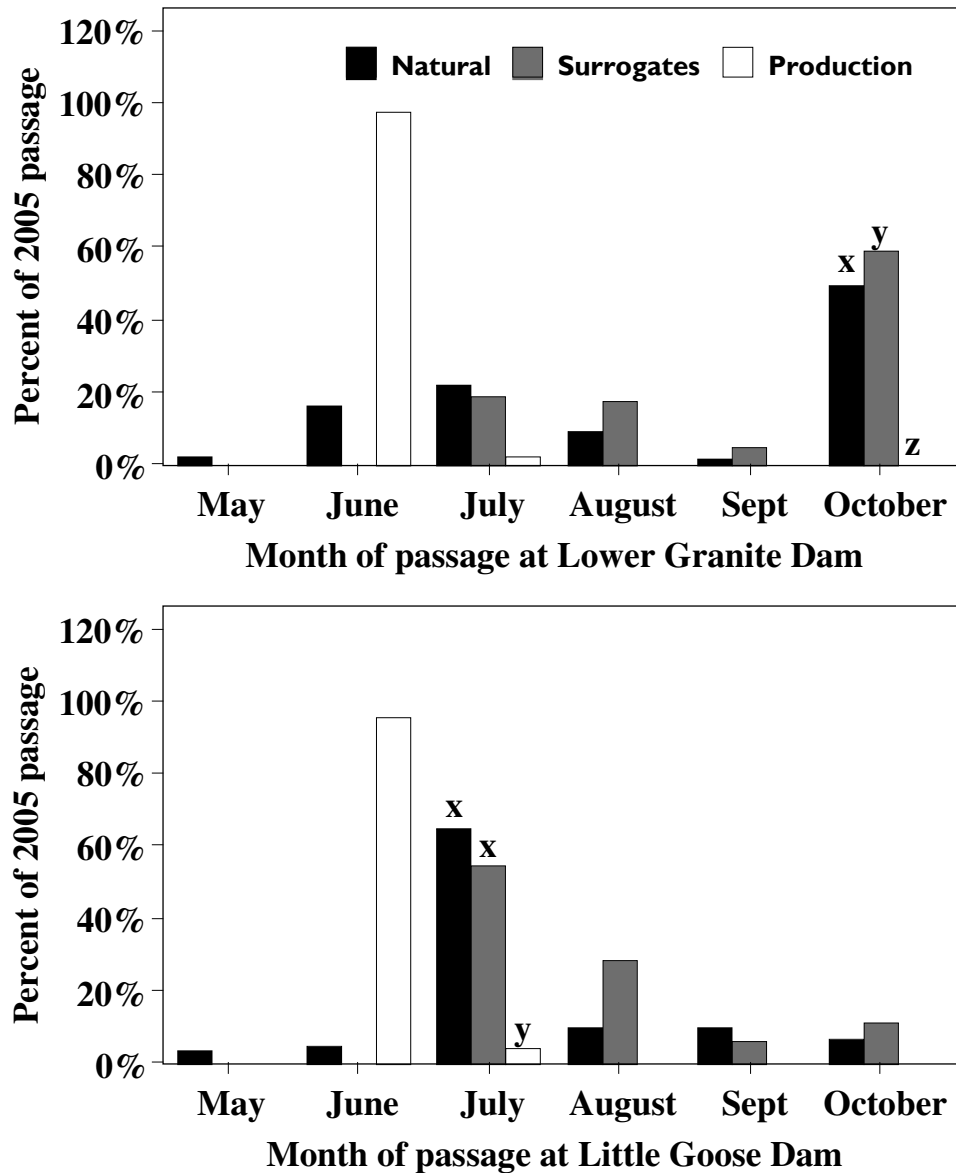


Figure 11. The percentage of the estimated number of Clearwater River natural, surrogate, and production subyearlings that passed Lower Granite, Little Goose, and Lower Monumental Dams during May–October, 2005. The different letters over the October (top panel) and July (bottom panel) passage bars indicate significant ($P < 0.05$) differences in passage among the three groups of subyearlings during the month of peak passage of natural subyearlings.

Exposure to Summer Spill

It is necessary to interpret the level of exposure to summer spill for Clearwater River natural and surrogate juveniles with the reservoir-type life history in mind. Passage estimates for Lower Granite Dam indicated that 22% of natural juveniles and 14% of surrogates that passed when the PIT-tag detection system was watered up had been reservoir-type juveniles. These reservoir-type juveniles, as well as those that passed during late fall and winter undetected, never experienced summer spill at Lower Granite Dam. Likewise, the passage timing analyses also showed that some natural and surrogate juveniles ceased migration after passing Lower Granite Dam and thus did not experience spill at Little Goose Dam. This was also the case for natural juveniles at Lower Monumental Dam, and to a very small extent for production subyearlings at all three dams.

The percentage of Clearwater River fish exposed to summer spill at Lower Granite Dam was 35% for natural subyearlings, 37% for surrogate subyearlings, and 9% for production subyearlings (Figure 12). The percentage of these fish exposed to summer spill at Little Goose Dam was 75% for natural subyearlings, 82% for surrogate subyearlings, and 16% for production subyearlings. The percentage of fish exposed to summer spill at Lower Monumental Dam was 100% for natural subyearlings, 84% for surrogate subyearlings, and 41% for production subyearlings.

Exposure to summer spill varied significantly among the three Clearwater River release groups (global $P = 0.005$) and among the three dams (global $P = 0.01$). There was no significant difference in the percentage of fish exposed to spill between natural and surrogate subyearlings (pair-wise $P = 0.9$), whereas a significantly lower percentage of production subyearlings were exposed to summer spill than natural (pair-wise $P = 0.004$) and surrogate subyearlings (pair-wise $P = 0.04$).

Travel Time to Lower Monumental Dam

Weighted mean travel time (\pm SE) to Lower Monumental Dam was 40 ± 1.0 d for Clearwater River surrogate subyearlings ($n^{2005} = 386$), and 21 ± 0.4 d for Clearwater River production subyearlings ($n^{2005} = 711$). The one Clearwater River natural subyearling detected at Lower Monumental Dam took 39 d from release to Lower Monumental Dam.

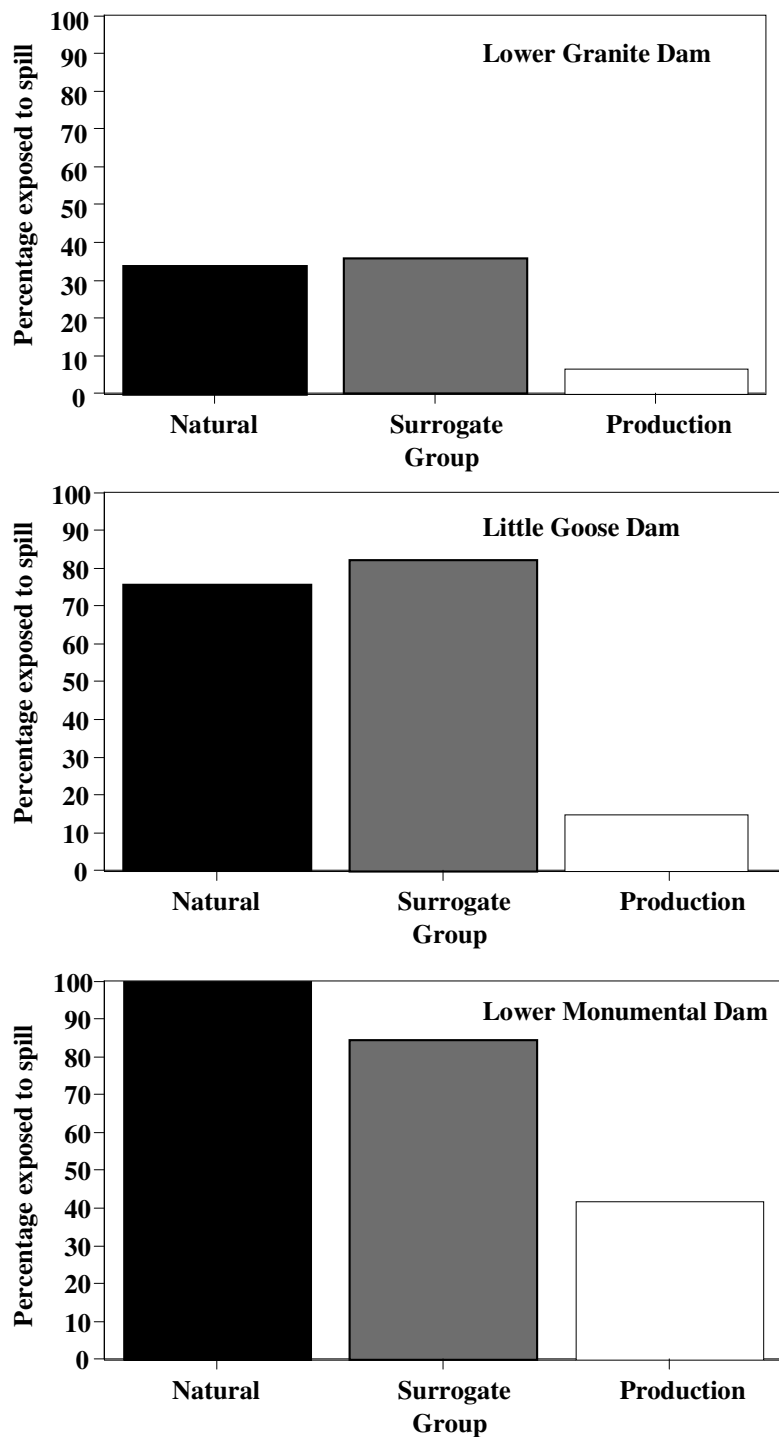


Figure 12. Estimated percentages of Clearwater River natural, surrogate, and production fall Chinook salmon that migrated as subyearlings that were exposed to spill in 2005 at Lower Granite (top panel), Little Goose (middle panel), and Lower Monumental (bottom panel) Dams.

Size During Migration

The only Clearwater River natural and surrogate subyearlings recaptured in 2005 were sampled by hook and line in Lower Granite Reservoir during fall (Table 4). These fish, which were likely to become reservoir-type juveniles, were large in fork length and robust (Table 4). We did not recapture any Clearwater River natural or surrogate subyearlings at Bonneville Dam in 2005 or any natural juveniles as yearlings in 2006 at Lower Granite or Bonneville Dam. The surrogates we recaptured in 2006 at Lower Granite and Bonneville Dams were large in fork length and robust.

Table 4. Mean length, weight, and condition factor of PIT-tagged Clearwater River natural, surrogate, and production subyearlings released in 2005 and then recaptured in Lower Granite Reservoir in 2005 and Lower Granite and Bonneville dams in 2006.

Recapture dam	Group	N	Recapture dates		Fork length (mm)	Weight (g)	Condition factor (K)
			Min	Max			
2005							
Lower Granite	Natural	2	02-Nov	06-Dec	180 ±2	64.6 ±2.3	1.12 ±0.00
	Surrogate	4	02-Nov	06-Dec	178 ±21	67.2 ±22.4	1.16 ±0.03
2006							
Lower Granite	Surrogate	47	28-Mar	12-May	203 ±19	96.3 ±29.8	1.12 ±0.07
Bonneville	Surrogate	32	06-Apr	21-Apr	208 ±19	97.5 ±26.0	1.06 ±0.08

Joint Probability of Migration and Survival

We could not estimate the joint probability of active migration and survival from release to the tailrace of Lower Monumental Dam (\pm SE) for Clearwater River natural subyearlings because the majority of these fish ceased migration or died after passing Lower Granite and Little Goose Dams in 2005. A similar situation was observed for Clearwater surrogates, but enough surrogate subyearlings passed Lower Monumental Dam and were detected downstream in 2005 to provide estimates for the 3 intra-annual release groups. Mean joint probability of active migration and survival to the tailrace of Lower Monumental Dam was $1.6 \pm 0.8\%$ for surrogate subyearlings and $41.8 \pm 3.3\%$ for Clearwater River production subyearlings ($N = 1$ intra-annual release groups).

Overall Comparison of Attributes

For Clearwater River fish, the similarity was greater between natural and surrogate than between natural and production subyearlings in all 11 attributes compared (Table 5). On average, there was a 1.4-fold difference in attributes between natural and surrogate subyearlings and a 57.8-fold difference in attributes between natural and production subyearlings. The null hypothesis rejection rate was 60% for tests between natural and surrogate subyearlings compared to 100% for tests between natural and production subyearlings.

Table 5. Similarity indices calculated by dividing the higher value of the attribute by lower value of the attribute for each comparison made between Clearwater River natural (Ns) and surrogate (S) subyearlings and between Snake River natural (Np) and production subyearlings (P). A value of 1.0 for an index equals similarity, 2.0 indicates a two-fold difference, etc. Results of hypothesis tests conducted between natural and surrogate subyearlings and between natural and production subyearlings are also given (yes, rejected H_0 ; no, failed to reject H_0).

Attribute	Ns	Np	S	P	Similarity indices		H ₀ rejected	
					S	P	S	P
Lower Granite Dam								
Cumulative passage	0.360	0.147	0.142	0.968	2.5	6.6	Yes	Yes
Peak monthly passage	0.493	0.493	0.589	0.000	1.2		Yes	Yes
Passage in 2006	0.219	0.219	0.1497	0.003	1.5	83.6	Yes	Yes
Exposure to spill	0.347	0.347	0.366	0.085	1.1	4.1	No	Yes
Little Goose Dam								
Cumulative passage	0.783	0.083	0.569	0.954	1.4	11.4	Yes	Yes
Peak monthly passage	0.650	0.650	0.543	0.044	1.2	14.8	No	Yes
Passage in 2006	0.574	0.574	0.385	0.002	1.5	237.0	Yes	Yes
Exposure to spill	0.750	0.750	0.824	0.163	1.1	4.6	No	Yes
Lower Monumental Dam								
Passage in 2006	0.890	0.890	0.680	0.0042	1.3	211.9	Yes	Yes
Exposure to spill	1.000	1.000	0.837	0.415	1.2	2.4	No	Yes
Travel time	39	39	40	21	1.0	1.9	N/A	N/A
Overall means and percentages					1.4 (10)	57.8 (10)	60%	100%

DISCUSSION

Differences in sampling efficiency across the season, and incomplete sampling of all rearing areas in the Snake and Clearwater rivers made collection of a representative sample of wild PIT-tagged fish somewhat difficult. Therefore, the wild portion of study fish comprise only a generally representative index of the overall population of naturally produced fall Chinook. Furthermore, the unknown proportion of subyearlings that disperse into Lower Granite Reservoir prior to growing to 60-mm fork length was not represented in the PIT-tag data collected on Snake and Clearwater River natural fall Chinook salmon.

Production subyearlings used in 2005 were not tagged in proportion to the numbers released at each location: production subyearlings released from Hells Canyon Dam were over-represented. Preliminary analyses were conducted prior to pooling the data from production fish to ensure that pooling did not mask any effects of release location, date, or size that would have changed our conclusions. Production subyearlings were marked in relative proportion to release numbers in 2006, and we will analyze data from these releases in 2007. Finally, we assumed that error in the estimates of detection probability were not the underlying factor for differences in observed passage timing, exposure to summer spill, and travel time among the three groups of subyearlings.

Snake River Natural and Surrogate Subyearlings

This research clearly illustrated the diverse juvenile life history of natural Snake River Basin fall Chinook salmon. Consistent with observations during several non-spill years (e.g., Connor et al. 2002; Marsh et al. 2007), natural juveniles from the population were present in the Lower Snake River hydropower system year-round. Some natural subyearlings migrated actively downstream during spring and early summer, whereas others migrated less actively in late summer and fall. Some natural subyearlings exhibited a reservoir-type juvenile life history by wintering in Lower Granite or Little Goose reservoirs and resuming seaward movement in spring 2006. An unknown portion of the natural reservoir-type juveniles ceased migration upstream from Lower Granite Dam and then dispersed downstream during winter, when the PIT-tag detection system was dewatered.

Evidence supporting the importance of juvenile life history diversity to production of Snake River Basin fall Chinook salmon is growing beyond the original findings of

Arnsberg and Statler (1995), Connor et al. (2002, 2005), and Marsh et al. (2007). To complete a rigorous and unbiased comparison of maximized inriver migration and maximized transport, large numbers of hatchery fall Chinook salmon subyearlings will have to be reared and released by use of a strategy designed to foster juvenile life history diversity.

We concluded that post-release attributes we studied in 2005 were more similar between Snake River natural and surrogate subyearlings than between Snake River natural and production subyearlings, with the exception of migrant size. There is, however, room for improvement in surrogate performance: on average, the difference in post-release attributes between natural and surrogate subyearlings was 2.3-fold for fish from the Snake River and 1.4-fold for fish from the Clearwater River. Hereafter, we discuss the second goal of our study, using the 2005 results to learn how to increase the similarity between natural and surrogate subyearlings. We also discuss the role of production subyearlings in the overall comparison of SARs for Snake River Basin fall Chinook salmon that pass downstream through the hydropower system under river operations that maximize inriver migration vs. those that pass under operations to maximize transport.

To increase similarity in dam passage timing, exposure to spill, travel time, and size during migration between natural and surrogate subyearlings, the two most plausible approaches are to release Snake River surrogates at smaller fork lengths and to release them during the planned 3-week release period. Migrational disposition is directly proportional to release size and inversely proportional to release date (Connor et al. 2000, 2003, 2004; Smith et al. 2003). If we had released Snake River surrogates at smaller sizes and made the third weekly release, the surrogate group as a whole might have passed the dams later, been exposed to more summer spill, had longer travel times, and exhibited the reservoir-type life history more frequently. Snake River surrogates might have been larger during seaward migration in 2005 if they had been released at a slightly smaller mean fork length, as smaller subyearlings spend more time feeding than actively migrating (Connor et al. 2004).

Altering release duration and size at release would likely also increase the similarity between Snake River natural and surrogate subyearlings in the joint probability of active migration and survival to the tailrace of Lower Monumental Dam. However, for Snake River surrogates, an increase in the joint probability of active migration and survival would require earlier release as well as larger size at release (e.g., Smith et al. 2003; Connor et al. 2004; results in this report). These two steps would contradict our previous recommendations.

Acclimation for extended periods is known to increase the survival of production subyearlings (S. Rosenberger, Idaho Fishery Resource Office, unpublished data), but acclimation facilities are presently operating at capacity under the production subyearling program. Providing Snake River surrogates of uniform size is a second feasible alternative for increasing survival. In 2005, it was necessary to reduce feed rations for Snake River surrogates to slow growth enough to achieve the 70-75 mm target size. This slowing was needed because nearly half of these fish were 65 mm or longer upon arrival at Dworshak National Fish Hatchery. The low condition factor at release of these fish in 2005 was a direct result of reduced feed levels. Reduced growth rates during rearing and the low condition factor at release may have contributed to the relatively low survival of Snake River surrogate subyearlings in 2005.

In 2006 and the future, we recommend a uniform size distribution for Lyons Ferry Hatchery subyearlings transferred to Dworshak National Fish Hatchery. This would ensure the large majority of fish were above the minimum fork length of 60 mm for tagging the first week of release, while preventing a shortage of 60-mm fish in the third week. Controlling growth and reducing mean fork length of surrogates is not feasible at Lyons Ferry Hatchery because the hatchery cannot rear surrogates without compromising the production subyearling program. However, transfer of eyed eggs from a single egg take at Lyons Ferry Hatchery to a second hatchery with colder incubation temperatures (e.g., Umatilla Hatchery) would be a feasible method to control size at release. After emergence, these subyearlings could be transferred as fry to Dworshak National Fish Hatchery. This would provide Dworshak National Fish Hatchery with a better opportunity to meet tagging and release schedules and to culture slightly smaller surrogates with a uniform size distribution.

Clearwater River Natural and Surrogate Subyearlings

For Clearwater River fish, the primary differences between natural and surrogate subyearlings were 1) dam passage was less protracted for natural than surrogate subyearlings, 2) far fewer natural than surrogate subyearlings were detected passing Lower Monumental Dam, and 3) natural subyearlings had higher percentages of reservoir-type juveniles detected passing the dams than surrogates.

The difference in dam passage timing between Clearwater River natural and surrogate subyearlings was quite possibly the result of seasonal changes in beach seining efficiency, which were obvious in the field. In contrast to the Snake River, where beach seines become more efficient as summer progresses, in the Clearwater River seines

become less efficient in early July, when summer flow is augmented from Dworshak Reservoir. These observations, combined with preliminary data, indicate that in July, a portion of the Clearwater River subyearling population moves rapidly downstream to the upper end of Lower Granite Reservoir, where some subyearlings discontinue downstream movement and rear for protracted periods.

We recommend trying a variety of sampling methods in 2006 and the future to capture subyearlings at the confluence of the Snake and Clearwater River. Successful PIT tagging of the later-rearing portion of the natural population will increase the sample size of natural subyearlings. This might increase the similarity in passage timing at the dams between natural and surrogate subyearlings.

The low number of natural subyearlings detected at Lower Monumental Dam could be a result of the relatively few Clearwater River natural subyearlings that were PIT-tagged. In 2005, use of screw traps and fyke nets as alternative capture methods to increase the number of subyearlings for tagging did produced promising results. These methods should be continued in the future in an effort to increase the number subyearlings detected at Lower Monumental Dam. The number of reservoir-type surrogate juveniles detected at the dams would likely be increased by adding a weekly release of surrogates in July.

Production Subyearlings

In 2005, we found an average 31.3-fold difference in post-release attributes between Snake River natural and production subyearlings and a 57.8-fold difference between Clearwater natural and production subyearlings. These differences were the result of production subyearlings responding to release in the wild as intended. Production subyearlings passed dams early, migrated rapidly, rarely exhibited a reservoir-type life history, and had a relatively high probability of active migration and survival.

In past years, production subyearlings were sometimes released at relatively small fork lengths and late in the season. This was partly the result of rearing problems and release practices that have since been overcome or discontinued at Lyons Ferry Hatchery. Late-season releases of smaller fish contributed to the misperception that production subyearlings might be suitable surrogates for natural subyearlings. Indeed, production subyearlings could represent natural subyearlings if they were released at 70-75 mm fork length (or smaller) from May to July, as we described for surrogate subyearlings, or

perhaps on a weekly basis as described by Smith et al. (2003). These changes in rearing and release strategies would have to be negotiated through *U.S. v. Oregon*.

We do not believe production subyearlings of 85–90 mm should be used to represent natural subyearlings that pass downstream through the hydropower system under strategies of maximum inriver migration or maximum transport. However, production subyearlings are presently an integral component of mitigation through the *Lower Snake River Compensation Plan*. Production subyearlings are cultured and released to mitigate lost harvest opportunity, and they play a large role in the Snake River Basin supplementation program. Thus, it seems prudent to conduct additional research to understand how SARs of production subyearlings are affected under the maximized inriver migration and maximized transport strategies. Increasing the number of production subyearlings that are PIT tagged, with emphasis on representing the population of production subyearlings within existing constraints, would provide this information. The tagging of representative groups of surrogate and production subyearlings would also allow comparison of SARs between these two types of hatchery subyearlings, which would be useful to supplementation planning.

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